ANNALS OF THE SOUTH AFRICAN MUSEUM

ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

VOLUME 73

BAND 73

ANNALS OF THE SOUTH AFRICAN MUSEUM
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VOLUME 73 BAND

THE TRUSTEES OF THE
SOUTH AFRICAN MUSEUM
CAPE TOWN

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  Address(es) of author(s) (institution where work was carried out)
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Fischer, P.-H., Duval, M. & Raffy, A. 1933. Études sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* **74**: 627–634.

Kohn, A. J. 1960*a*. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) **2**: 309–320.

Kohn, A. J. 1960*b*. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* **17** (4): 1–51.

Thiele, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. *In:* Schultze, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* **4**: 269–270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* **16**: 269–270.

(*continued inside back cover*)

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HYDROIDS FROM THE KERGUELEN AND CROZET SHELVES, COLLECTED BY THE CRUISE MD.03 OF THE *MARION-DUFRESNE*

By

N. A. H. MILLARD

Cape Town Kaapstad

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By

N. A. H. Millard

South African Museum, Cape Town

(With 12 figures and 2 tables)

[*MS. accepted 28 December 1976*]

ABSTRACT

Thirty-four species of hydroids are described from the Kerguelen and Crozet groups of islands, including two new species: *Halecium dufresneae* and *Zygophylax crozetensis*. Among them are five cosmopolitan species. The rest show affinities partly with the cold-temperate Magellan Region of South America, and partly with Antarctica. The fauna is considered to be subantarctic in nature.

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INTRODUCTION

The cruise MD.03 of the *Marion-Dufresne* during the period 18 March to 28 April 1974 to the Kerguelen and Crozet groups of islands was intended as a preliminary reconnaissance of the area to serve as a basis for a more detailed survey. The cruise was highly successful in the quantity and variety of benthic invertebrates taken, and although the subsequent cruises MD.04 (1975) and MD.08 (1976) have now been completed, it may be some time before the hydroid material is all sorted and worked up. It was felt that the publication of the present results should not be delayed.

The cruise was financially and logistically supported by the Terres Australes et Antarctiques Françaises, Paris. The bulk of the material and the types of the new species will be deposited in the Muséum National d'Histoire Naturelle, and a few duplicates are being retained at the South African Museum.

The cruise MD.03 was described by the Chef de la Campagne, J. C. Hureau (1976), who also gave a complete station list and a chart of the voyage. The positions of the stations yielding hydroid material are, however, repeated here for convenience.

Ann. S. Afr. Mus. **73 (1)**, 1977: 1–47, 12 figs, 2 tables.

The Kerguelen Shelf lies in the southern Indian Ocean at approximately 50°S and 70°E. Kerguelen is the largest island, Heard and MacDonald lying about 644 km to its south-east. The depths from which hydroids were taken range from 6 to 790 m, the abyssal dredgings from over the edge of the plateau yielding no hydroid material.

The Crozet Shelf (including among others the Ile de la Crozet, Île de la Possession and Île aux Cochon) lies some 1 930 km to the west of Kerguelen, and hydroids were dredged from depths of 110 to 400 m.

STATION LIST

2/6. E. Kerguelen; 4.4.74; 49°30,7′S 70°44,7′E; 115 m: *Zygophylax crozetensis, Symplectoscyphus subarticulatus.*

2/7. E. Kerguelen; 4.4.74; 49°33,2′S 70°47,1′E; 130 m: *Symplectoscyphus subarticulatus.*

3/10. E. Kerguelen; 5.4.74; 49°28,5′S 71°52,8′E; 650 m: *Eudendrium tottoni, Modeeria rotunda, Opercularella belgicae, Lafoea dumosa, Plumularia insignis.*

3/11. E. Kerguelen; 5.4.74; 49°25,4′S 71°51,7′E; 620–650 m: *Eudendrium tottoni, Modeeria rotunda, Filellum serratum, Lafoea dumosa, Symplectoscyphus subdichotomus, Plumularia insignis.*

7/22. N.E. Heard; 7.4.74; 52°12,7′S 75°38,4′E; 525–560 m: *Staurotheca dichotoma, Plumularia insignis.*

8/24. N. Heard; 8.4.74; 52°58,0′S 73°42,0′E; 123 m: *Campanularia norvegiae, Staurotheca dichotoma, Sertularella picta, Symplectoscyphus elongatus, S. mawsoni.*

8/25. N.E. Heard; 8.4.74; 52°59,4′S 73°38,0′E; 90 m: *Modeeria rotunda, Staurotheca dichotoma, Symplectoscyphus elongatus, S. subdichotomus, Schizotricha unifurcata.*

9/26. Heard, Atlas Cove; 8.4.74; 15–20 m: *Sertularella picta, Schizotricha unifurcata.*

9/27. Heard, Atlas Cove; 8.4.74; 6 m: *Sertularella picta.*

10/30. S.S.E. MacDonald; 9.4.74; 53°06,7′S 72°50,1′E; 255 m: *Modeeria rotunda, Symplectoscyphus mawsoni, Schizotricha unifurcata.*

11/31. W. Heard; 9.4.74; 53°20,3′S 72°29,2′E; 790 m: *Staurotheca dichotoma.*

14/44. W. Kerguelen; 13.4.74; 49°48,4′S 64°57,9′E; 250 m: *Symplectoscyphus plectilis, S. subdichotomus.*

14/45. W. Kerguelen; 13.4.74; 49°45,8′S 64°50,6′E; 262 m: *Hydrodendron arborea, Staurotheca dichotoma, Symplectoscyphus subarticulatus.*

17/50. N.W. Kerguelen; 14.4.74; 47°24,9′S 66°04,0′E; 585 m: *Kirchenpaueria triangulata, Plumularia insignis.*

18/52. N.W. Kerguelen; 15.4.74; 47°42,2′S 68°07,1′E; 243 m: *Modeeria rotunda, Plumularia insignis.*

21/57. N.E. Kerguelen; 15.4.74; 48°29,7′S 70°55,4′E; 345–360 m: *Zygophylax crozetensis, Staurotheca dichotoma, Symplectoscyphus subdichotomus, Plumularia insignis.*

22/58. N.E. Kerguelen; 16.4.74; 48°58,5′S 70°51,1′E; 90–105 m: *Eudendrium rameum, Halecium tenellum, Zygophylax crozetensis, Staurotheca dichotoma, Sertularella picta, Symplectoscyphus subdichotomus, Schizotricha unifurcata.*

23/59. S.E. Kerguelen; 16.4.74; 49°59,2′S 70°01,9′E; 158 m: *Eudendrium rameum, Staurotheca dichotoma, Plumularia insignis, Schizotricha unifurcata.*

24/61. S.E. Kerguelen; 17.4.74; 50°10,7′S 69°48,7′E; 195 m: *Tulpa diverticulata, Staurotheca dichotoma, Plumularia insignis.*

26/63. Crozet, chenal des Orques; 20.4.74; 46°21,5′S 51°55′E; 230 m: *Modeeria rotunda, Phialella chilensis, Halecium dufresneae, Filellum serratum, Zygophylax crozetensis, Campanularia* sp., *Staurotheca dichotoma, Symplectoscyphus curvatus, S. subdichotomus.*

26/64. Crozet, chenal des Orques; 20.4.74; 46°24′S 51°59′E; 180 m: *Eudendrium rameum, Modeeria rotunda, Phialella chilensis, Hydrodendron arborea, Grammaria abietina, Halisiphonia ?nana, Hebella striata, Zygophylax crozetensis, Campanularia* sp., *Tulpa diverticulata, Staurotheca antarctica, S. dichotoma, Sertularella picta, Symplectoscyphus curvatus, S. elongatus, S. subdichotomus, Oswaldella bifurca, Plumularia insignis.*

26/65. Crozet, chenal des Orques; 21.4.74; 46°23,3′S 51°58,3′E; 165 m: *Symplectoscyphus subdichotomus.*

28/71. Entre Possession et Cochons; 22.4.74; 46°18,1′S 51°29′E; 400 m: *Halecium delicatulum, H. jaederholmi, Sertularella picta, Symplectoscyphus subdichotomus.*

30/73. Entre Possession et Cochons; 22.4.74; 46°02,3′S 50°50,2′E; 187 m: *Tulpa diverticulata, Staurotheca antarctica, S. dichotoma, Symplectoscyphus subdichotomus, Plumularia insignis.*

31/74. Entre Possession et Cochons; 22.4.74; 45°57,2′S 50°32,8′E; 110 m: *Modeeria rotunda, Phialella chilensis, Halecium jaederholmi, Hydrodendron arborea, Grammaria abietina, Zygophylax crozetensis, Silicularia rosea, Tulpa diverticulata, Staurotheca antarctica, S. dichotoma, Sertularella geodiae, S. picta, Symplectoscyphus subdichotomus.*

SYSTEMATIC SECTION

Family **Eudendriidae**

Eudendrium rameum (Pallas, 1766)

Eudendrium rameum: Allman, 1888: 4, pl. 2 (figs 1–2). Vervoort, 1946: 150, figs 60–61. Vervoort, 1972*a*: 21.

Stations

22/58–C; 23/59–E; 26/64–P. All fertile.

Description

Stiff, bushy colonies with thick, fascicled stems reaching a maximum height of 120 mm and a diameter of 5 mm at base, branching irregularly and in all planes. Maximum diameter of unfascicled stems 0,26 mm. Perisarc annulated on origin of branches, partly or completely on hydranth pedicels, and at other irregular intervals, brown in colour. Hydranth with about 20 tentacles, with abundant large nematocysts on hypostome and in nettle ring.

Male gonophores borne on non-atrophied hydranths, one- to two-chambered. Female gonophores borne on non-atrophied hydranths, young ones with unbranched spadix.

Large nematocysts: microbasic euryteles very similar to those illustrated by Weill (1934, fig. 66); 19,8 × 9,0 — 25,8 × 10,8 μm, discharged shaft 20,4–24,0 μm.

Remarks

Totton (1930) considered that all Antarctic material of *Eudendrium* should be included in one species: *E. antarcticum* Totton = *E. tottoni* Stechow. Totton included Jäderholm's (1905) material from South Georgia doubtfully in this species; and it presumably follows that Allman's (1888) material from

Kerguelen Island should be included too, since Jäderholm said that the two samples were very similar.

In the present collection, however, there are almost certainly two species of *Eudendrium*, a delicate form with a flexuous stem (*E. tottoni*) and a stiff bushy form which the author has assigned to *E. rameum*. Unfortunately the former is not well enough preserved for examination of nematocysts, which must provide the final evidence, but the latter possesses abundant large microbasic euryteles, a type which according to J. Bouillon (personal communication) is characteristic of *E. rameum*. The bushy colony is also very similar to Vervoort's (1946) illustration of *E. rameum*.

Eudendrium tottoni Stechow, 1932

Eudendrium ramosum: Vanhöffen, 1910: 288, fig. 13.
Eudendrium antarcticum Totton, 1930: 140.
Eudendrium tottoni: Rees & Thursfield, 1965: 62.

Stations

3/10–E; 3/11–A. (Both fertile.)

Description

Delicate colonies reaching a height of about 16 mm. Stems unfascicled or weakly fascicled at base, flexuous, difficult to distinguish from hydrorhiza, branching irregularly, about 0,08 mm in diameter. Groups of annulations present on origins of branches and rarely at other points. Hydranths poorly preserved.

Female gonophores with unbranched spadix arching over a single egg. Male gonophores one- to two-chambered.

Remarks

The hydranths in this species are too poorly preserved to distinguish structure or number of tentacles, though the gonophores have survived. The tentacles of the fertile hydranths appear to be persistent. *E. tottoni* is known from a number of localities in the Antarctic.

Family **Campanulinidae**

Modeeria rotunda (Quoy & Gaimard, 1827)

Stegopoma fastigiatum: Vervoort, 1972*a*: 42.
Modeeria rotunda: Edwards, 1973: 573, figs 1–3. Millard, 1975: 137, fig. 45A.

Stations

3/10–C; 3/11–G; 8/25–D; 10/30–C; 18/52–B; 26/63–B; 26/64–G; 31/74–M.

Description

Many infertile colonies epizootic on other hydroids. Hydrotheca and pedicel extremely variable in size.

Remarks

This is a new record for this area. The species has, however, been recorded from the south-western Atlantic at a very similar latitude (Vervoort 1972*a*).

Opercularella belgicae (Hartlaub, 1904)

Figure 1B

Campanulina belgicae Hartlaub, 1904: 10, pl. 1 (figs 8–9). Vanhöffen, 1910: 308, fig. 28.
Opercularella belgicae: Leloup, 1974: 4, fig. 2.
Opercularella sp. Vervoort, 1972*a*: 42, fig. 11b, c.

Station

3/10–F.

Description

A sparse colony without gonothecae growing on a polyzoan. Colony stolonic. Pedicels of very variable length, with 2–4 spiral annulations at base, merging smoothly into hydrotheca. Hydrotheca deep, widest at opercular base, with about eight opercular segments and a delicate diaphragm.

Measurements (mm)

Total height, pedicel + hydrotheca	1,00–6,90
Hydrotheca, height from diaphragm to tip of operculum ..	0,46–0,57
maximum diameter	0,16–0,20

Remarks

Vervoort's material (1972*a*: *Opercularella* sp.) from Magellan is very similar to the present material, though with shorter pedicels. It appears to fall within the range of variation of *O. belgicae*.

The generic name of this species is still provisional pending knowledge of the gonophore.

Phialella chilensis (Hartlaub, 1905)

Figure 1A

Campanulina chilensis Hartlaub, 1905: 589, fig. L^2, M^2, N^2. Naumov & Stepaniants, 1962: 76, fig. 3. Leloup, 1974: 3, fig. 1.
Phialella chilensis: Vervoort 1972*a*: 38, fig. 10.

Stations

26/63–H; 26/64–Q; 31/74–N.

Description

Slender stems, a few lightly fascicled at base, branching sympodially and reaching a maximum height of 10,8 mm. Stem closely annulated in basal half of each internode and smooth in distal half, as illustrated by Vervoort (1972*a*) rather than by Hartlaub (1905). Hydrothecal pedicels completely annulated or with a smooth area in the centre of the longer ones. Hydrotheca as in previous descriptions. Gonothecae absent.

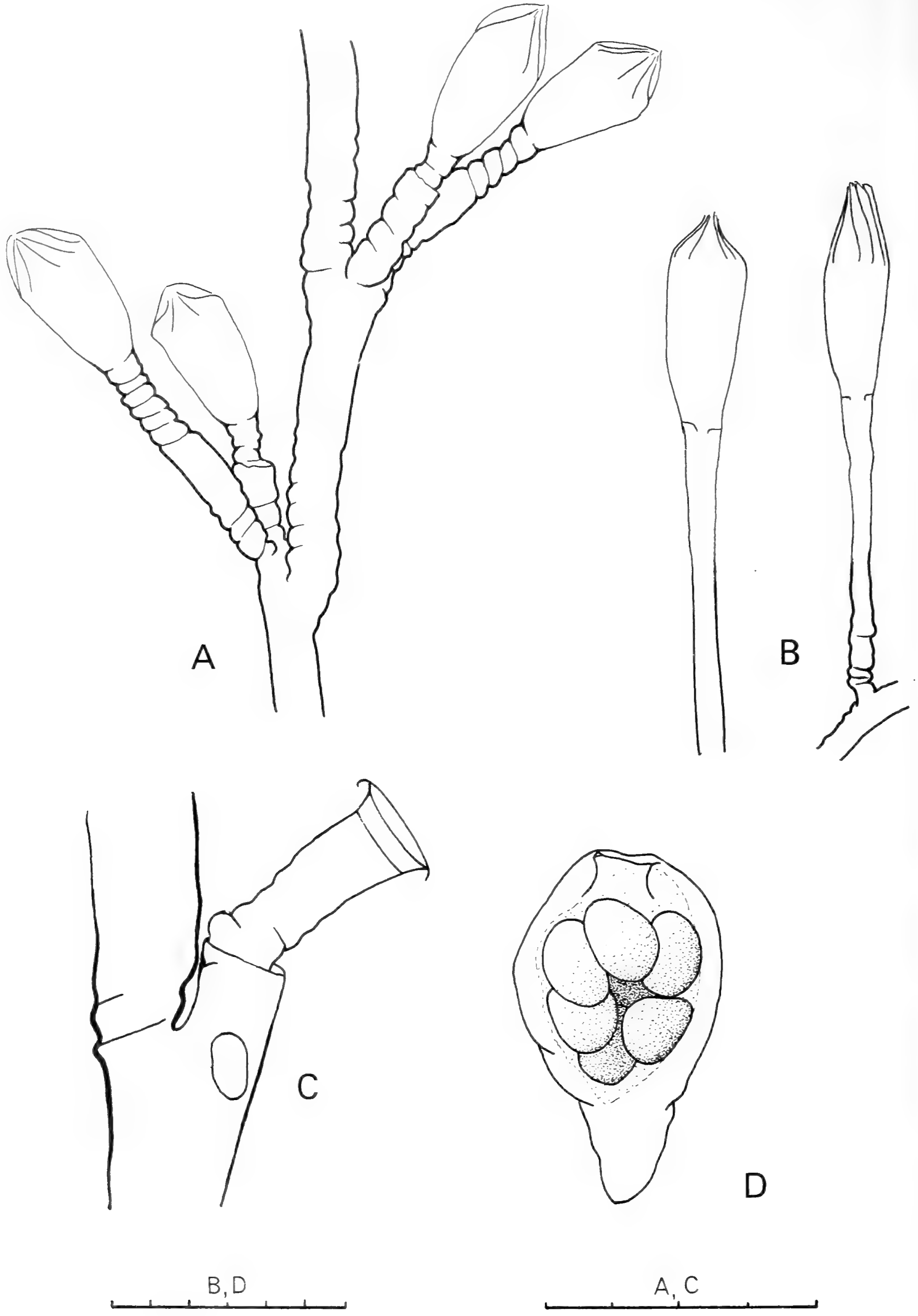

Fig. 1.

Phialella chilensis (Hartlaub). A. Part of stem with hydrothecae.
Opercularella belgicae (Hartlaub). B. hydrothecae.
Halecium delicatulum Coughtrey. C. Hydrophore. D. Gonophore.

Scale in mm/10.

Measurements (mm)

Hydrotheca, height from diaphragm to tip of operculum ..	0,21–0,29
maximum diameter	0,11–0,14

Remarks

This species is well known from the Antarctic and Subantarctic, especially from the South American area. This is the first record from the Kerguelen region.

Family **Haleciidae**

Halecium delicatulum Coughtrey, 1876

Figure 1C–D

Halecium delicatulum: Ralph, 1958: 334, figs 11e, h–n, 12a–p. Naumov & Stepaniants, 1962: 94, fig. 16. Vervoort, 1972*b*: 341, fig. 2a.
Halecium antarcticum Vanhöffen, 1910: 317, fig. 34. Billard, 1914: 7, fig. 5. Totton, 1930: 144, fig. 4.

Station

28/71–B.

Description

A number of stems growing on a gorgonian and reaching 32 mm in height. Stem fascicled and stiff, branching irregularly. Internodes separated by oblique nodes sloping in alternate directions, with one or two annulations at the base of each. Primary hydrophores free from stem, smooth, sometimes containing a pseudodiaphragm. Secondary hydrophores annulated, at least in basal region. Hydrothecal margin strongly flared outward.

Female gonothecae present, compressed, oval in broad view, with terminal aperture surrounded by an internal collar of perisarc, containing 6–10 eggs.

Measurements (mm)

Internode length	0,53–0,72
Hydrotheca, depth to diaphragm	0,03–0,06
diameter at margin	0,17–0,20
Gonotheca, length	0,71–1,12
maximum diameter	0,35–0,52

Remarks

The author has bowed to the opinion of Naumov & Stepaniants (1962) and Vervoort (1972*b*) in including *H. antarcticum* in the synonymy of *H. delicatulum*, although she feels that there is a distinct Antarctic form in which the female gonotheca is smaller and more slender and without the 'ears' of typical *H. delicatulum* as illustrated by Millard (1975). The gonothecae in the present material are similar to those illustrated by Totton (1930) and Vervoort (1972*b*).

H. delicatulum is well known from the Antarctic, particularly in the area south of America, and was reported from Marion Island by Allman (1888, as *H. flexile*).

Halecium dufresneae sp. nov.

Figure 2A–D

Material

Holotype: from Station 26/63–A. Part in Muséum National d'Histoire Naturelle, Paris, and part in the South African Museum (SAM–H2785).

Description of holotype

One colony, with a thick rootstock flattened below and a thick fascicled stem 245 mm in height. Stem branching and rebranching irregularly but mainly in one plane. Final branches unfascicled, divided into internodes by oblique nodes sloping in alternate directions, each internode bearing a hydrotheca from an apophysis at distal end.

Primary hydrophore not clearly demarcated from apophysis, with a stout pseudodiaphragm in base, adnate to internode almost to diaphragm. Secondary hydrophores rather rare in this material, smooth and not constricted after origin, asymmetrical with adcauline wall longer than abcauline, with or without a pseudodiaphragm. Hydrotheca shallow, with adcauline surface free from stem, with margin usually everted.

Gonothecae borne on sides of hydrophores, the two series together forming a single row on the anterior surface of the stem. Gonotheca flattened, in broad view widening to the truncated distal end, with one or two large embryos discharged into a marsupium which may be as large as, or larger than, itself.

Measurements (mm)

Internode, length	0,51–1,00
Hydrotheca, depth from diaphragm	0,03–0,07
diameter at margin	0,19–0,23
Gonotheca, depth	0,94–1,14
maximum diameter	0,38–0,64
Marsupium, depth	0,66–1,14

Remarks

Female gonothecae with external marsupia are known from two other species of *Halecium*, namely *H. pallens* Jäderholm, 1904, from South Georgia, and *H. marsupiale* Bergh, 1887, from the Arctic.

The author feels that in these two, as in the present species, the marsupium is an important diagnostic character, and she cannot agree with Naumov & Stepaniants (1962) and Vervoort (1972*b*) who include *H. pallens* in the synonymy of *H. delicatulum*. A marsupium has never been seen in the latter; moreover

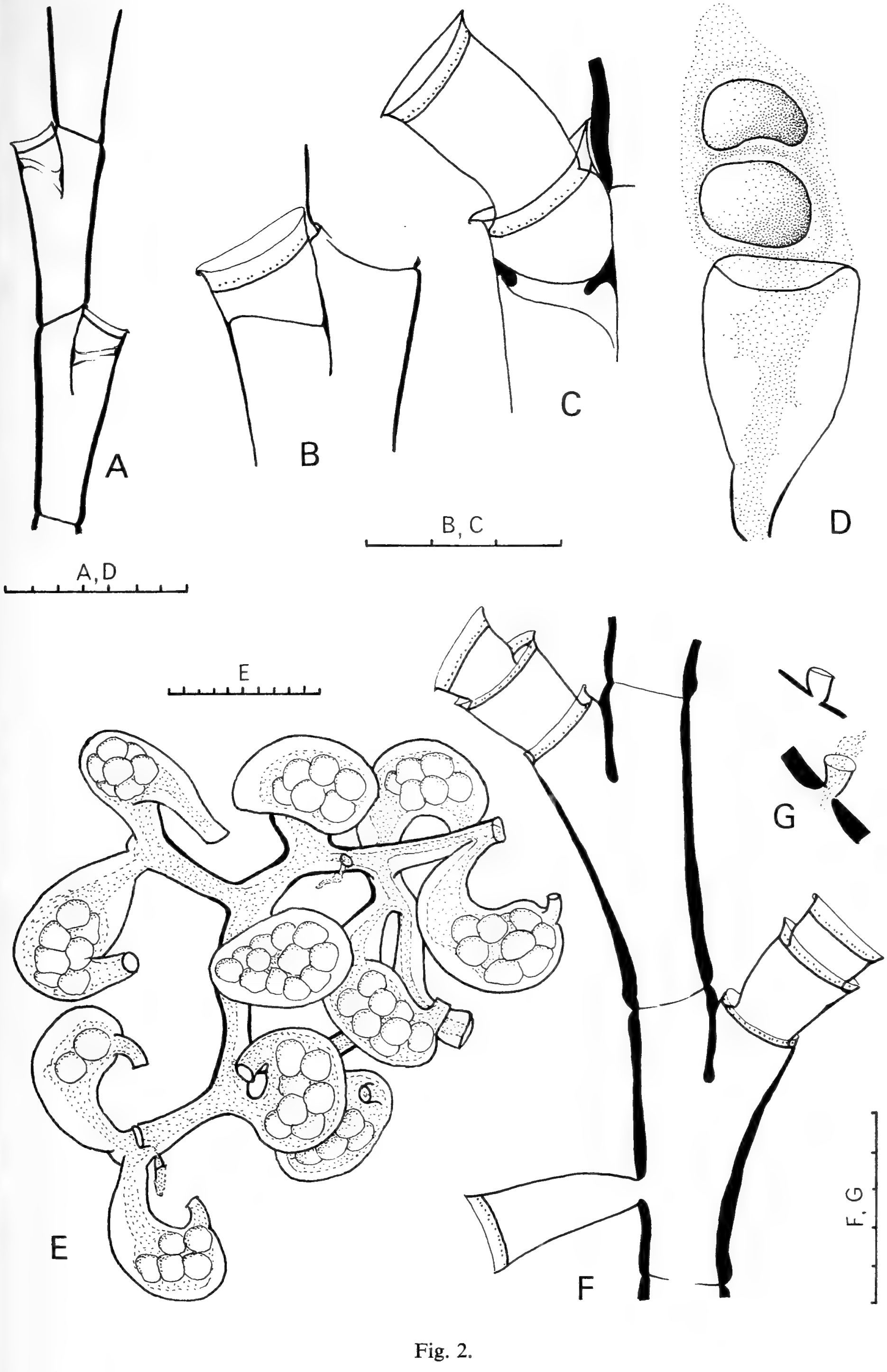

Fig. 2.

Halecium dufresneae sp. nov. from the holotype. A–C. Parts of stem with hydrophores: C with secondary hydrophore. D. Gonophore with two embryos in marsupium.
Hydrodendron arborea (Allman). E. part of glomulus with female gonophores. F. Part of stem with hydrophores and a giant nematotheca on bottom left. G. normal nematothecae.

Scale in mm/10.

the shape of the mature female gonotheca is different, being wider in broad view and 'eared' in *H. delicatulum.*

It follows that it is not possible to identify most of the species of ***Halecium*** from sterile material alone.

The present species differs from *H. pallens* in the shorter pedicel of the primary hydrophore and in the marsupium, which is almost as large as, or larger than, the gonotheca and contains only one or two eggs.

Halecium jaederholmi Vervoort, 1972

Figure 3A–B

Halecium jaederholmi Vervoort, 1972*a*: 21, fig. 2 (synonymy).

Stations

28/71–A; 31/74–A.

Description

The first colony (28/71–A) is medium-brown in colour, with thick fascicled stems 4 mm in diameter at the base and 160 mm in maximum height, branching irregularly and in all planes. The second colony (31/74–A) is dark brown and has an even thicker main stem (8 mm diameter at base) and is more stiff and rigid in habit. It reaches a height of 140 mm.

In both colonies the unfascicled parts together with their internodes and hydrophores have a structure exactly like that illustrated by Vervoort (1972*a*) except that no pseudodiaphragmata are present nor any secondary hydrophores. The hydrothecae are very shallow and adnate to the internodes.

Typical female gonothecae are present in the first colony and contain up to six larvae; some of the gonothecae are damaged and broken off transversely just beyond the aperture. In the second colony all the gonothecae (female) are damaged in this way.

Measurements (mm)

Internode, length	0,50–0,94
Hydrotheca, depth to diaphragm	0,03–0,04
diameter at margin	0,17–0,23
Gonotheca, length	1,49–1,85
maximum diameter	0,59–0,71

Remarks

The distribution of this species has been summarized by Vervoort; it occurs in the Antarctic and Subantarctic, but this is the first record from the Kerguelen area.

Halecium tenellum Hincks, 1861

Halecium tenellum: Millard, 1975: 156, fig. 50F–L. Cornelius, 1975: 409, fig. 12.

Station

22/58–D.

Description

Colony epizootic on a polyzoan, with sparsely branched stems reaching 8 mm in height, and with female gonophores.

Remarks

This cosmopolitan species has been reported from the south-western Atlantic and from Antarctica. This is the first record from the Kerguelen area.

Hydrodendron arborea (Allman, 1888)

Figure 2E–G

Halecium robustum Allman, 1888: 10. Vervoort, 1972*a*: 23.
Halecium arboreum Allman, 1888: pl. 4. Hickson & Gravely, 1907: 27, pl. 4 (figs 27–29).
Ophiodissa arborea: Totton, 1930: 142, fig. 2a. Vervoort, 1972*a*: 25.

Stations

14/45–B; 26/64–N; 31/7–J. All colonies fertile.

Description

Shrubby colonies with thick, fascicled stems reaching a maximum height of 105 mm. Branching very irregular; final branches divided into internodes by oblique nodes slanting in alternate directions. Each internode bearing one hydrophore on an apophysis at distal end. Primary hydrophore not distinctly demarcated from apophysis, adnate to internode almost, or completely, to level of diaphragm.

Primary hydrotheca with free adcauline wall, with margin sometimes everted on adcauline side. Secondary hydrophores usually quite symmetrical, with no constriction after origin.

Nematothecae goblet-shaped, normally one on each internode on side opposite to hydrotheca, but often broken off leaving only the aperture, and sometimes absent without trace; also present on tubes of gonosome. Occasionally giant nematothecae present, about five times the size of normal ones.

Gonothecae borne in glomulus (term from Naumov 1960: 442), strongly curved, with tubular neck, containing eggs or planulae. Glomuli forming large masses about 15 mm in diameter.

Measurements (mm)

Internode, length	0,42–0,93
Hydrotheca, depth to diaphragm	0,04–0,07
diameter at margin	0,21–0,28

Measurements (mm)

Normal nematotheca, depth	0,06–0,10
Giant nematotheca, depth	0,44–0,48
Gonotheca, maximum length	0,78–1,02
maximum diameter	0,47–0,60

Remarks

This species is widely distributed in the Antarctic; its type locality is Kerguelen.

As other authors have remarked, the nematothecae are variable in occurrence and not invariably present on each internode. The giant nematothecae have not been recorded before. The regenerated (secondary) hydrophores are very distinctive and clearly distinguish the species from forms such as *H. beanii.*

Family **Lafoeidae**

Filellum serratum (Clarke, 1879)

Filellum serratum: Vervoort, 1972*a*: 51, fig. 14a–b. Millard, 1975: 178, fig. 59A–C.

Stations

3/11–F; 26/63–J: infertile colonies epizootic on polyzoa and other hydroids.

Remarks

This cosmopolitan species has not yet been reported from the Kerguelen area, though it is known from New Zealand and South America.

Grammaria abietina (Sars, 1850)

Figure 3D–E

Grammaria abietina: Cornelius, 1975: 382, fig. 3 (synonymy).

Stations

26/64–K; 31/74–L.

Description

Two colonies with thick, fascicled stems reaching a maximum height of 83 mm and branching in an alternate, subopposite or opposite manner in one plane. Hydrothecae forming six longitudinal rows on stem and branches, but not strictly regular in arrangement.

Hydrotheca curved outwards to a varying degree, with margin everted and either parallel or oblique to axis of stem; free part 0,34–0,51 mm in length; 0,28–0,35 mm in diameter at margin.

A single coppinia present, about 15 mm long and 5 mm wide. Gonothecae tightly adpressed, flask-shaped, with terminal aperture on a short tubular neck. Accessory tubes about three times length of gonothecae, very strongly curved.

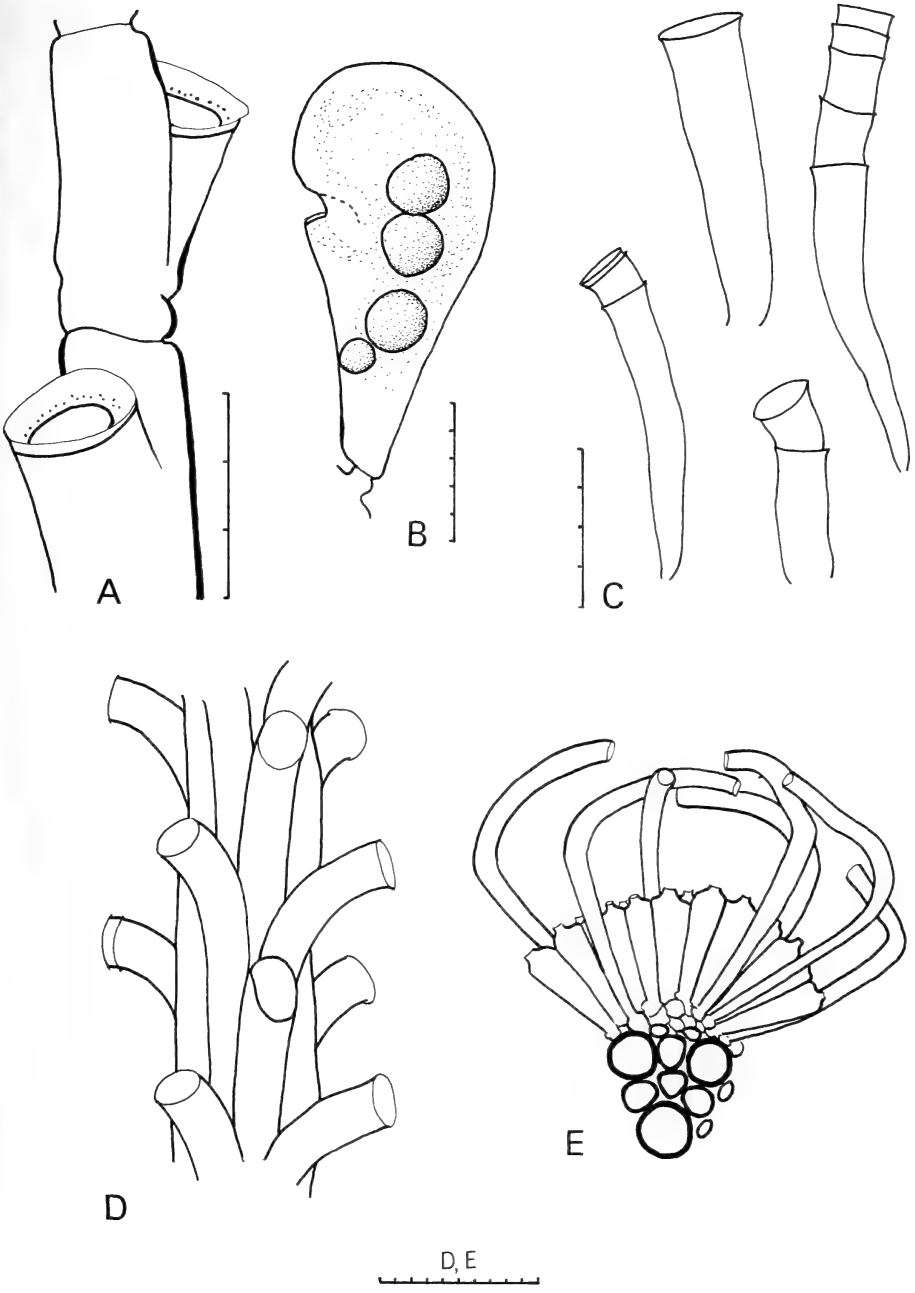

Fig. 3.

Halecium jaederholmi Vervoort. A. Part of stem with two hydrophores. B. Gonophore.
Halisiphonia ?nana Stechow. C. Hydrothecae.
Grammaria abietina (Sars). D. Part of stem with six rows of hydrothecae. E. Part of t.s. of coppinia, showing gonothecae, protective structures, and arrangement of thecal bases in three's in centre of stem.

Scale in mm/10.

Remarks

The synonymy of this species was recently revised by Cornelius (1975), who has included as synonyms *G. stentor* Allman, 1888, *G. magellanica* Allman, 1888, and *G. insignis* Allman, 1888.

The species has a bipolar distribution and is widely known from the Arctic and Subarctic as well as from the Antarctic and Subantarctic. The type locality of *G. stentor* is Kerguelen Island.

Halisiphonia ?nana Stechow, 1921

Figure 3C

Halisiphonia nana: Stechow, 1925: 452, fig. 22.

Station

26/64–S.

Description

An infertile colony epizootic on *Sertularella picta*. Pedicel arising from hydrorhiza and merging smoothly into hydrotheca which widens evenly to margin. No diaphragm or annular thecal thickening. Margin sometimes slightly everted.

Measurements (mm)

Pedicel + hydrotheca, height	0,64–0,95
Pedicel, diameter at base	0,04–0,12
Hydrotheca, diameter at margin	0,14–0,23

Remarks

This material is assigned with some doubt to *H. nana*. The dimensions are more or less in agreement with those of Stechow, and are too small for *H. megalotheca* Allman, but the pedicel is often rather wide at the base and the thecal margin may be everted. *H. nana* has been reported only once, from east of Bouvet Island; the gonothecae are unknown.

Hebella striata Allman, 1888

Hebella striata Allman, 1888: 30, pl. 15 (figs 3, 3a). Vanhöffen, 1910: 313. Vervoort, 1972*a*: 62, fig. 17b–c.

Station

26/64–R.

Description

An infertile colony epizootic on *Grammaria abietina*. Details exactly as in Vervoort's material, but dimensions a little larger.

Measurements (mm)

Pedicel, length	0,44–0,87
Hydrotheca, depth	0,77–1,10
diameter	0,24–0,31

Remarks

This species is known mainly from the Subantarctic near South America, but was reported from Kerguelen by Vanhöffen (1910).

Lafoea dumosa (Fleming, 1820)

Lafoea fruticosa: Millard, 1975: 187, fig. 61A–F.
Lafoea dumosa: Cornelius, 1975: 385, fig. 4 (synonymy).

Stations

3/10–B; 3/11–B. Both colonies infertile.

Description

Stems flexuous, reaching a maximum height of 78 mm, with many fragments.

Remarks

The author has followed Cornelius (1975) in uniting *L. fruticosa* (M. Sars, 1851), *L. gracillima* (Alder, 1856) and *L. dumosa* under the last name.

Zygophylax crozetensis sp. nov.

Figure 4

Material

Holotype: from station 26/64–B. Part in Muséum National d'Histoire Naturelle, Paris, and part in the South African Museum (SAM–H2779).

Other stations: 2/6–A (infertile); 21/56–C (infertile); 22/58–B (male); 26/23–D (fertile); 31/74–F (fertile).

Description of holotype

A large, branching colony 220 mm in height. Rootstock a large mass of interwoven fibres flattened below and reaching 45 mm in diameter. Stem fascicled and thick, giving off thick primary branches in an irregular fashion and mainly in one plane, these branches giving off secondary and tertiary branches which are strictly in one plane. Final branches (hydrocladia) sub-opposite in arrangement, lightly fascicled or unfascicled. Hydrocladia and final terminations of other branches segmented where exposed, with one or two hydrothecae to an internode, but with many irregular regenerative nodes. Hydrothecae normally alternate in arrangement with the two rows more or less in one plane, and this arrangement characteristic of unfascicled hydrocladia

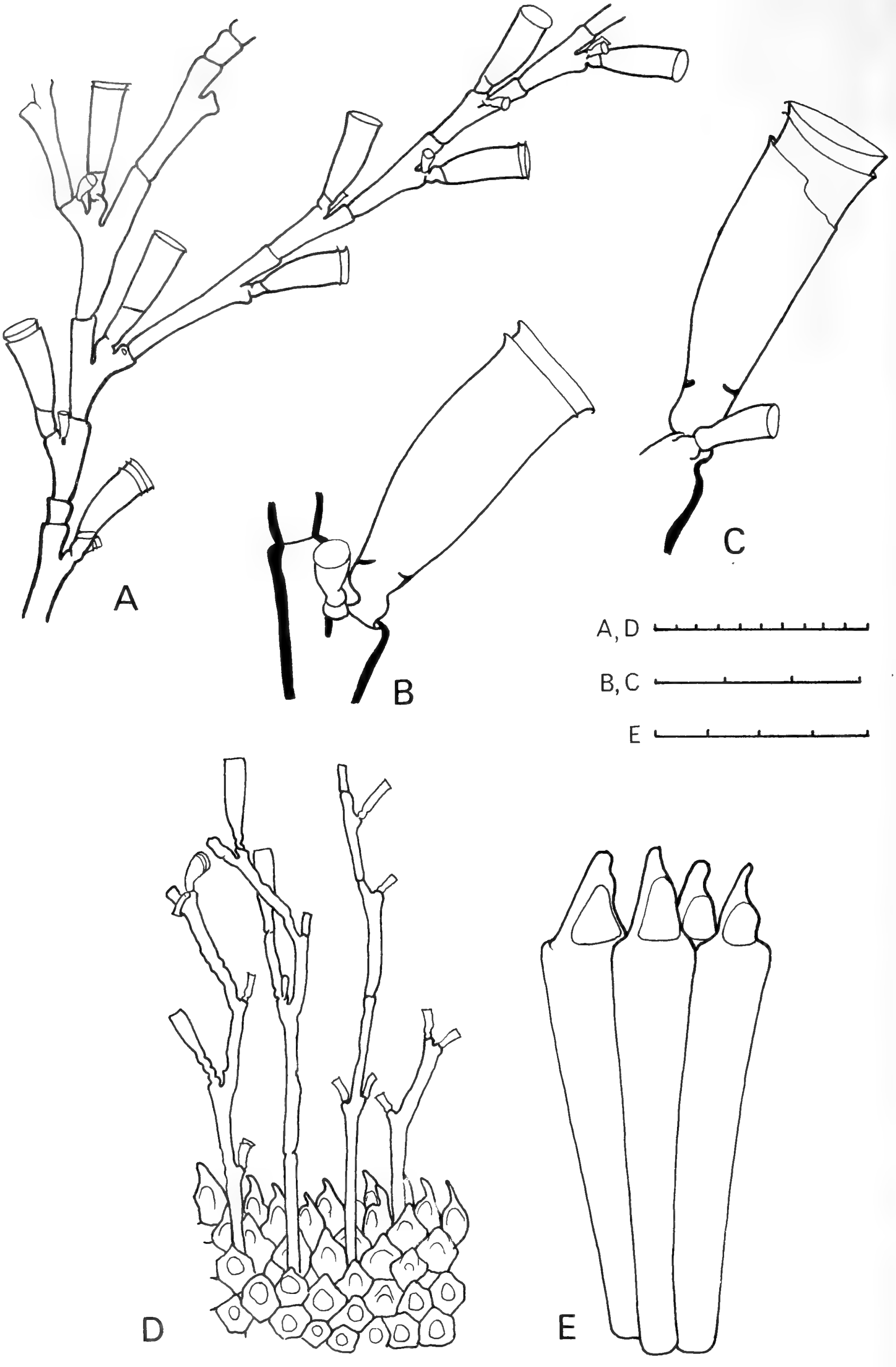

Fig. 4.

Zygophylax crozetensis sp. nov. from the holotype. A. Part of stem showing origins of hydrocladia. B–C. Hydrothecae and nematothecae. D. Surface view of coppinia showing hoods of gonothecae and protective structures. E. Gonothecae from t.s.

Scale in mm/10.

and smaller branches, but in fascicled branches supplementary hydrothecae may arise from peripheral tubes in any plane and in any position imparting a very irregular appearance to the whole.

Hydrothecae tubular, widening to margin which is slightly everted, curved outwards, those in axils of hydrocladia less curved and practically straight. Diaphragm distinct and oblique.

Nematothecae two-chambered, with a short basal chamber and a long tubular distal chamber, one or two on each hydrotheca-bearing apophysis, that/those of the axillary hydrotheca shifted on to the apophysis next to it, various irregular supplementary ones present on peripheral tubes of stem and branches.

Coppiniae numerous and clothing most of the larger branches completely to a width of 3–5 mm, so that it is not possible to distinguish one from another. Coppinia consisting of adpressed gonothecae with between them irregular branching structures bearing nematothecae and rarely hydrothecae as well. Gonotheca slender, widening distally to top of adnate part, then narrowing to a free, pointed, and sometimes curved, hood or horn bearing an aperture on one side. Sex not determinable.

Measurements of holotype (mm)

Hydrothecal pedicel, height	0,06–0,13
Hydrotheca, height abcauline	0,32–0,38
diameter at margin	0,16–0,20
Pedicel + hydrotheca, height	0,40–0,47
Nematotheca, height	0,09–0,19
diameter at margin	0,05–0,08

Remarks

In the four fertile samples all the gonothecae are of the same shape. Most, however, are empty. Contents are present in 22/58–B only, and these are male.

The hydrothecae of this species are similar to those of *Z. africana* Stechow, 1923, and a number of related species, and particularly to '*Lafoea*' *halecioides* Allman, 1874 (= '*Lafoea*' *pinnata* Sars, 1873). The last-mentioned, however, has an open coppinia with unfused gonothecae.

Nutting (1905) described and figured a closed coppinia with one-horned gonothecae for a species which he called *Lictorella halecioides*. This is apparently a synonym for *Zygophylax antipathes* (Lamarck, 1816), and not for *Z. pinnata*. It is probably this account which prompted Totton (1930: 166) to mention 'hooded apertures' for *Z. antipathes* and not the account of Trebilcock (1928) who does not mention the species. However, *Z. antipathes* has somewhat broader hydrothecae than the present material, and the gonothecae as depicted by Nutting have terminal apertures.

It appears that a number of southern hemisphere species of *Zygophylax* have similar trophosomes but different gonosomes. The gonothecae of the present species are almost exactly like those of *Cryptolaria pectinata* (Allman, 1888).

Family **Campanulariidae**

Campanularia norvegiae Broch, 1948

Figure 5A–E

Campanularia norvegiae Broch, 1948: 16, fig. 5.

Station

8/24–E.

Description

A dense fertile colony growing on an empty tube. Hydrorhiza reticular. Pedicel sometimes spirally grooved throughout, but very variable and often smooth in certain areas, always with a segment of lesser diameter at distal end. Hydrotheca funnel-shaped, oval in section and thickened, more so at the narrow ends; thickened at, or just below, margin.

Gonotheca irregularly bottle-shaped, with a short annulated pedicel, narrowing distally to terminal aperture, often twisted or irregularly corrugated, circular in section, empty or containing planulae.

Measurements (mm)

Pedicel + hydrotheca, length	1,70–8,50
Hydrotheca, depth	0,48–0,72
maximum diameter (broad view)	0,38–0,56
Gonothecal pedicel, depth	0,24–0,32
Gonotheca, depth	1,58–2,28
maximum diameter	0,52–0,65

Remarks

This species is distinguished from the closely related *C. integra* MacGillivray, 1842, by the shape of the gonotheca. Since the gonothecae contain planulae it is obvious that no medusoid is released.

C. norvegiae was originally described from South Georgia.

Campanularia sp.

Figure 5F

Stations

26/63–G; 26/64–R.

Description

Infertile colonies epizootic on other hydroids. Pedicels of variable length, with one terminal spherule of lesser diameter, generally roughly corrugated

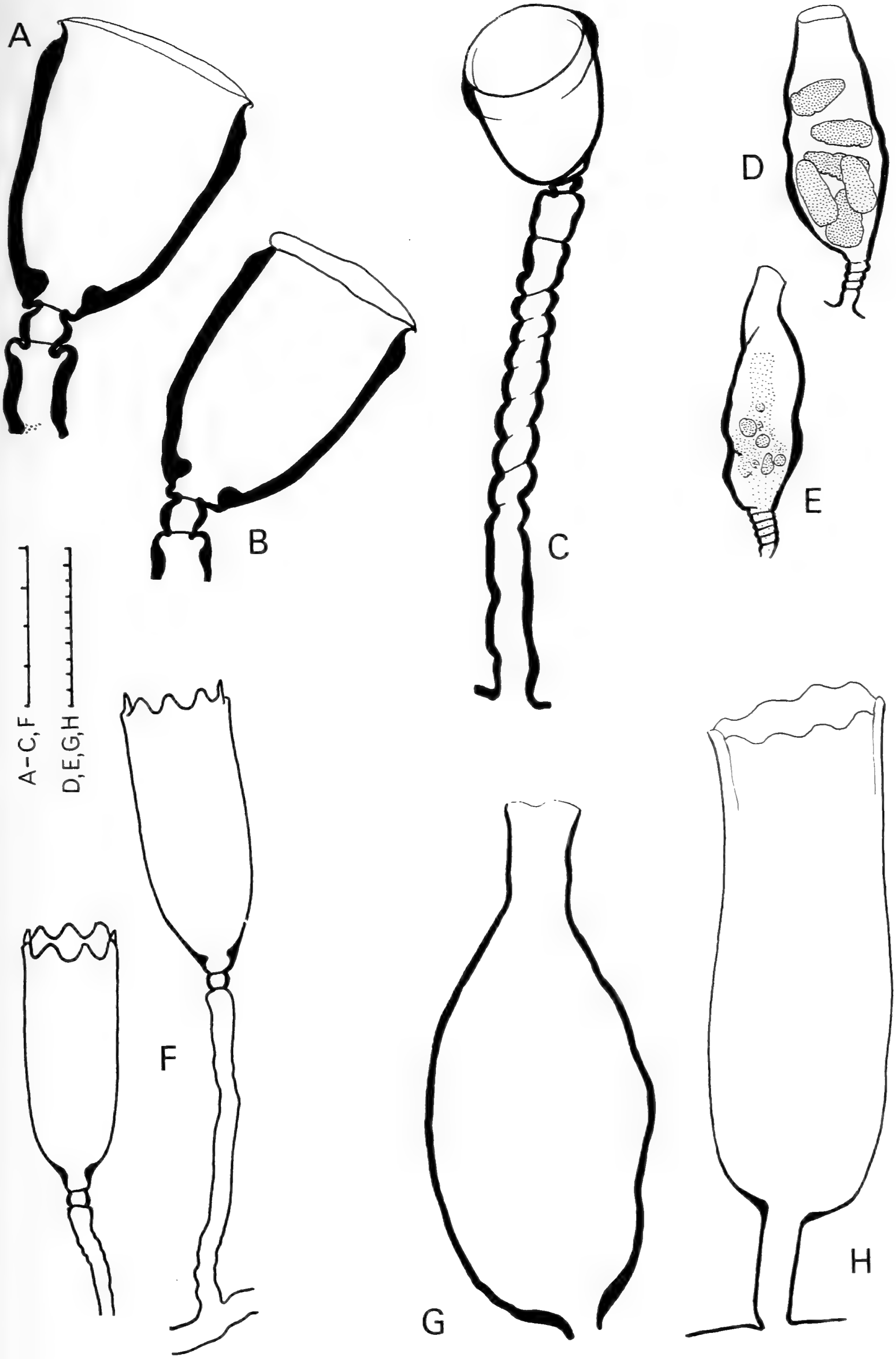

Fig. 5.

Campanularia norvegiae Broch. A–C. Hydrothecae. D–E. Gonophores.
Campanularia sp. F. Hydrothecae.
Tulpa diverticulata Totton. G. Gonotheca. H. Hydrotheca.

Scale in mm/10.

immediately below this and at base. Hydrotheca deep, with parallel sides, with an annular thickening near base, with 8–10 slender, bluntly rounded marginal teeth.

Measurements (mm)

Pedicel, length	0,48–1,07
Hydrotheca, depth	0,60–0,90
diameter at margin	0,25–0,33
diameter/depth	0,34–0,51

Remarks

In the absence of gonophores this species cannot be definitely diagnosed. The two most commonly reported species of *Campanularia* from the Antarctic are *C. hicksoni* Totton, 1930, and *C. tincta* Hincks, 1861. (*C. cylindrica* Allman, 1876, from Kerguelen is probably a synonym of the former.) These two species are distinguished mainly by their gonothecae—smooth in the former, annulated in the latter; however, none of the Antarctic material attributed to *C. tincta* has yet been found with gonothecae and possibly only one species is involved.

Silicularia rosea Meyen, 1834

Silicularia rosea: Ralph, 1956: 293. Millard, 1968: 259. Millard, 1971: 405.
Silicularia bilabiata: Ralph, 1956: 285, figs 2–3. Ralph, 1957: 842.

Station

31/74–C.

Description

A rich, fertile colony on brown alga.

Remarks

S. rosea is known from Crozet and Kerguelen Islands and many other localities in the Antarctic and Subantarctic. The distribution was summarized by Ralph (1957).

Tulpa diverticulata Totton, 1930

Figure 5G–H

Tulpa diverticulata Totton, 1930: 145, fig. 5. Ralph, 1957: 844, fig. 7l–n.
Campanularia diverticulata: Naumov & Stepaniants, 1962: 72.

Stations

24/61–C; 26/64–H; 30/73–A; 31/74–B.

Description

Hydrorhiza creeping on other hydroids, polyzoa and worm tubes, but often becoming free to form a tangled mass. Hydrothecal pedicels of very variable length, unsegmented, though often with regeneration nodes. Hydrothecae as in previous descriptions; regenerated margins sometimes present. Gonothecae arising from hydrorhiza on very short pedicels, irregularly oval, with terminal aperture on long narrow neck.

Measurements (mm)

Hydrothecal pedicel, length	0,60–2,80
Hydrotheca, length	3,00–4,10
diameter at margin	0,95–1,35
Gonotheca, length including pedicel	1,85–3,45
maximum diameter	0,89–1,50

Remarks

Some of these colonies are very rich, and several stolons may run together or twine round each other simulating a fascicled stem. However, the pedicels always arise at right angles, and there is never any question of an erect branching stem with oblique pedicels as in *T. tulipifera* (Allman, 1888). It is clear that these are two separate species.

Very fine cross-striations may be present on some of the hydrothecae and gonothecae in certain colonies.

Young gonothecae are cone-shaped and similar to those described by Fraser (1944) for *T. speciosa* (Clarke).

T. diverticulata is so far known only from New Zealand and to the south of it. It is a new record for Kerguelen and Crozet Islands. The closely related *T. tulipifera* occurs in Heard Island (Allman 1888) and in the south-western Atlantic (Vervoort 1972*a*).

Family **Syntheciidae**

Staurotheca antarctica Hartlaub, 1904

Staurotheca antarctica Hartlaub, 1904: 16, pl. 1 (fig. 4), pl. 2 (fig. 4). Totton, 1930: 176, 178, fig. 28, pl. 2 (fig. 6). Vervoort, 1972*a*: 198, figs 67, 68b.

Stations

26/64–M (fertile); 30/73–B (fertile); 31/74–D.

Description

Luxurious colonies with unfascicled stems which branch dichotomously and reunite to form an elaborate reticulum in one plane. Nodes irregular. Hydrothecae generally arranged in decussate pairs, but rarely in groups of three, and with many irregularities.

Male and female gonothecae present, as in previous descriptions.

Measurements (mm, all without regenerations)

Hydrotheca, depth abcauline	0,34–0,44
depth adcauline, adnate part	0,38–0,50
depth adcauline, free part	0,10–0,20
adnate part/total adcauline depth	0,66–0,83
diameter at mouth	0,17–0,20
Gonotheca, male, length	0,84–1,12
maximum diameter	0,55–0,66
Gonotheca, female, length	1,30–1,48
maximum diameter (including spur)	0,98–1,21

Remarks

There is little to add to the description of this well-known Antarctic and Subantarctic species. Vervoort (1972*a*) has summarized the distribution.

Staurotheca dichotoma Allman, 1888

Staurotheca dichotoma Allman, 1888: 76, pl. 36 (fig. 1). Billard, 1910: 27, figs 11–12. Billard, 1914: 15, fig. 9. Totton, 1930: 175, 178, fig. 27.

Stations

7/22–B; 8/24–A (fertile: female gonophores); 8/25–B (fertile: male and female gonophores); 11/31–A; 14/45–A; 21/57–B (fertile: female gonophores); 22/58–G; 23/59–A (fertile: male gonophores); 24/61–B; 26/63–C; 26/64–L; 30/73–C (fertile: female gonophores); 31/74–E (fertile: female gonophores).

Description

Luxuriant colonies. Stems thick, fascicled at base in larger colonies, branching in a subdichotomous manner, reaching a maximum height of 130 mm. Hydrothecae generally 3 to a whorl (and forming 6 longitudinal rows), but some of the thickest stems have 4 to a whorl (and 8 longitudinal rows) and the thinner terminal branches only 2 (4 longitudinal rows). Hydrothecae adnate for almost their entire length. Male and female gonothecae as described by Billard (1910) and Totton (1930).

Measurements 8/25–B (mm)

Hydrotheca, depth abcauline	0,59–0,67
depth, adcauline, adnate part	0,78–0,96
depth adcauline, free part	0,03–0,08
adnate part/total adcauline depth	0,91–0,97
diameter at margin	0,27–0,32
Gonotheca, female, length	1,49–2,17
maximum diameter	1,11–1,29
Gonotheca, male, length	1,23–1,60
maximum diameter	0,78–1,02

Remarks

As previous authors have remarked, *S. dichotoma* is clearly distinguished from *S. antarctica* by the structure of the female gonotheca and by its greater dimensions. The species is widely distributed in the Antarctic and Subantarctic. Its type locality is Marion Island, not far from the present localities.

Family **Sertulariidae**

Sertularella geodiae Totton, 1930

Figure 6E–F

Sertularella geodiae Totton, 1930: 196, fig. 43, pl. 3 (figs 7–8). E. A. Briggs, 1939: 37. Ralph, 1961: 831, fig. 24c, g. Vervoort, 1972*a*: 120, fig. 37.

Station

31/74–K.

Description

A number of infertile stems and fragments, reaching a maximum height of 40 mm. Stem stiff, fascicled and straight at base, geniculate in terminal regions only, branching rather sparsely and in one plane. Branches unfascicled, arising below hydrothecae and, when several are present, below every third hydrotheca.

Hydrotheca adnate for about half adcauline wall, bent outwards (a perpendicular dropped through centre of margin passes through adcauline wall), with a few undulations on free part of adcauline wall, with wide mouth. No internal teeth.

Measurements (mm)

Internode length	1,01–1,52
diameter at node	0,20–0,32
Hydrotheca, length abcauline	0,66–0,77
length adcauline, adnate part	0,49–0,61
length adcauline, free part	0,46–0,60
adnate part/total adcauline length	0,46–0,55
diameter at margin	0,35–0,40

Remarks

This material is in many ways intermediate between *S. geodiae* and *S. conica* Allman, 1877, considering especially Vervoort's description of the latter (1972*a*: 123). However, *S. conica* has an unfascicled stem and a hydrotheca which narrows more markedly to the mouth; its distribution is mainly tropical. The author has therefore assigned this material to *S. geodiae* in spite of the absence of gonothecae; this is a species known from New Zealand, Tasmania

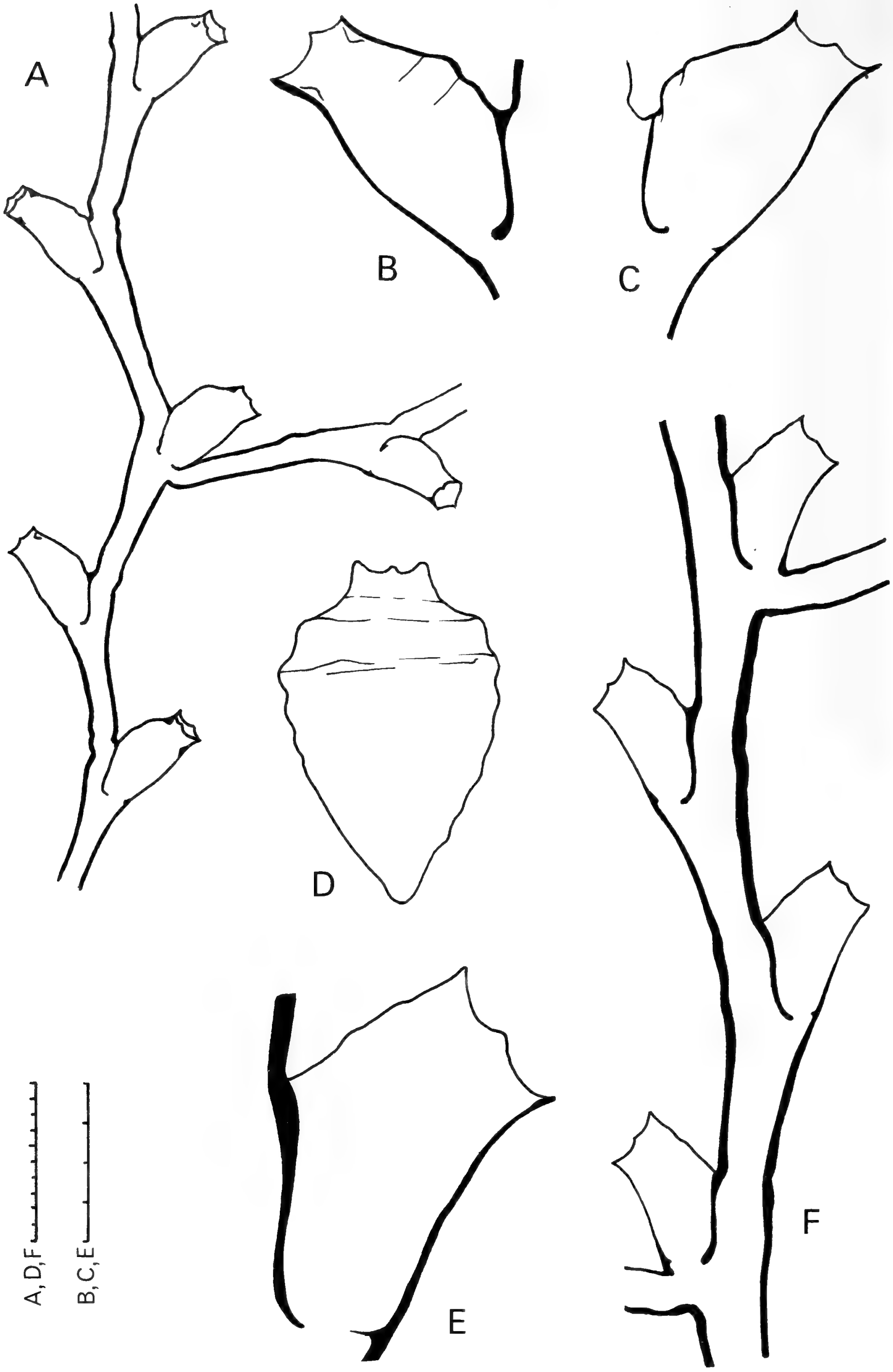

Fig. 6.

Sertularella picta (Meyen). A. Part of stem showing origin of a hydrocladium. B–C. Hydrothecae. D. Gonotheca.
Sertularella geodiae Totton. E. Hydrotheca. F. Part of stem showing origins of two hydrocladia.

Scale in mm/10.

and the area around the southern tip of South America, but which has not been reported from Kerguelen.

Sertularella picta (Meyen, 1834)

Figure 6A–D

Sertularella picta: Hartlaub, 1905: 645, fig. L^4. Billard, 1922: 106, fig. 2B. Stechow, 1923: 187, fig. B^1. Millard, 1971: 405, fig. 6A, B. Vervoort, 1972*a*: 111, figs 34, 35.

Stations

8/24–D; 9/26–A; 9/27–A; 22/58–E; 26/64–F; 28/71–D; 31/74–H. The last three fertile.

Description

Stems slender and straggling, branching repeatedly in an irregular fashion to produce tangled colonies often intertwined with polyzoans and with *Symplectoscyphus subdichotomus*. Stem normally unfascicled, but rarely with one or two supplementary tubes in basal region, usually with one or two annulations at base and on origin of branches, geniculate, reaching a maximum height of 38 mm, often reuniting by stolons with other stems. On most stems the two rows of hydrothecae are in the same plane, but in other stems, or even in other parts of the same stem, they may be shifted on to the anterior surface so that the two rows subtend an obtuse angle between them. Branches arising below hydrothecae, with one or two annulations at origin and a long first internode, otherwise similar to stem and of same diameter. Internodes slender, very variable in length, separated by oblique nodes sloping in alternate directions, usually with an annulation immediately above each node.

Hydrotheca fusiform, adnate for less than half adcauline height, narrowed below margin. In most hydrothecae the marginal teeth are equally developed and the margin is perpendicular to the axis (a perpendicular dropped through centre of margin passes through basal thickening of adcauline wall), but in some the abcauline marginal tooth is produced so that the margin is tilted towards the stem (and a perpendicular dropped through centre of margin passes through the hydrophore or base of the abcauline wall). All intergradations may occur in one colony. The free part of the adcauline wall usually has two to four indistinct annulations, but the latter are of variable development—they may form distinct striations which pass round the sides of the hydrotheca almost to the abcauline wall, or they may be almost obsolete. Small internal teeth are present in most hydrothecae, but again the degree of development is variable; the full complement appears to be three (one median abcauline and two latero-adcauline), but one or two, or even all three, may be absent. In a few stems there is no trace of internal teeth.

Gonothecae borne on front of stem immediately below hydrothecae, obovate, with three to four distinct annulations in distal half, with three or four blunt marginal spines, with external marsupium. Sex not determinable.

Measurements (mm)

Internode, length	0,77–1,34
diameter at node	0,12–0,18
Hydrotheca, length abcauline	0,55–0,70
length adcauline, adnate part	0,24–0,35
length adcauline, free part	0,40–0,51
adnate part/total adcauline length	0,33–0,44
diameter at margin	0,20–0,26
Gonotheca, length	1,50–2,15
maximum diameter	1,30–1,52

Remarks

The identification of this species has been based mainly on Vervoort's work (1972*a*), who also found considerable variability in structure. The form of the colony, the shape of the hydrotheca and the gonotheca are very similar to his material.

The species is known from the Falkland/Tierra del Fuego region, and was also reported from Marion Island (Millard 1971). The Marion Island material differs in the smooth hydrothecal wall and the greater displacement of the two rows of hydrothecae.

Symplectoscyphus curvatus (Jäderholm, 1917)

Figure 7A–C

Sertularella curvata Jäderholm, 1917: 9, pl. 1 (figs 11–12).
Symplectoscyphus curvatus: Totton, 1930: 192, fig. 40, pl. 2 (figs 1–3). E. A. Briggs, 1939: 31.
Sertularella curvatus: Naumov & Stepaniants, 1972: 45, fig. 7.

Stations

26/63–E; 26/64–C. Both infertile.

Description

Many unrooted, unfascicled stems and fragments yellow-brown in colour and reaching a maximum length of 44 mm. Most stems pinnate, geniculate, giving off alternate branches at each elbow and immediately below every third hydrotheca. On the proximal part of the stem the nodes are not clearly demarcated and the hydrothecae are well spaced and do not overlap, but on the distal part and on the branches the nodes are distinct and the tip on one hydrotheca overlaps the base of the next. The two rows of hydrothecae and branches in one plane.

Hydrotheca tubular, large, adnate for less than half adcauline length, curved outwards, not narrowing to mouth and with diameter in centre region approximately equal to that at margin, marginal teeth well developed, no internal teeth. No gonothecae.

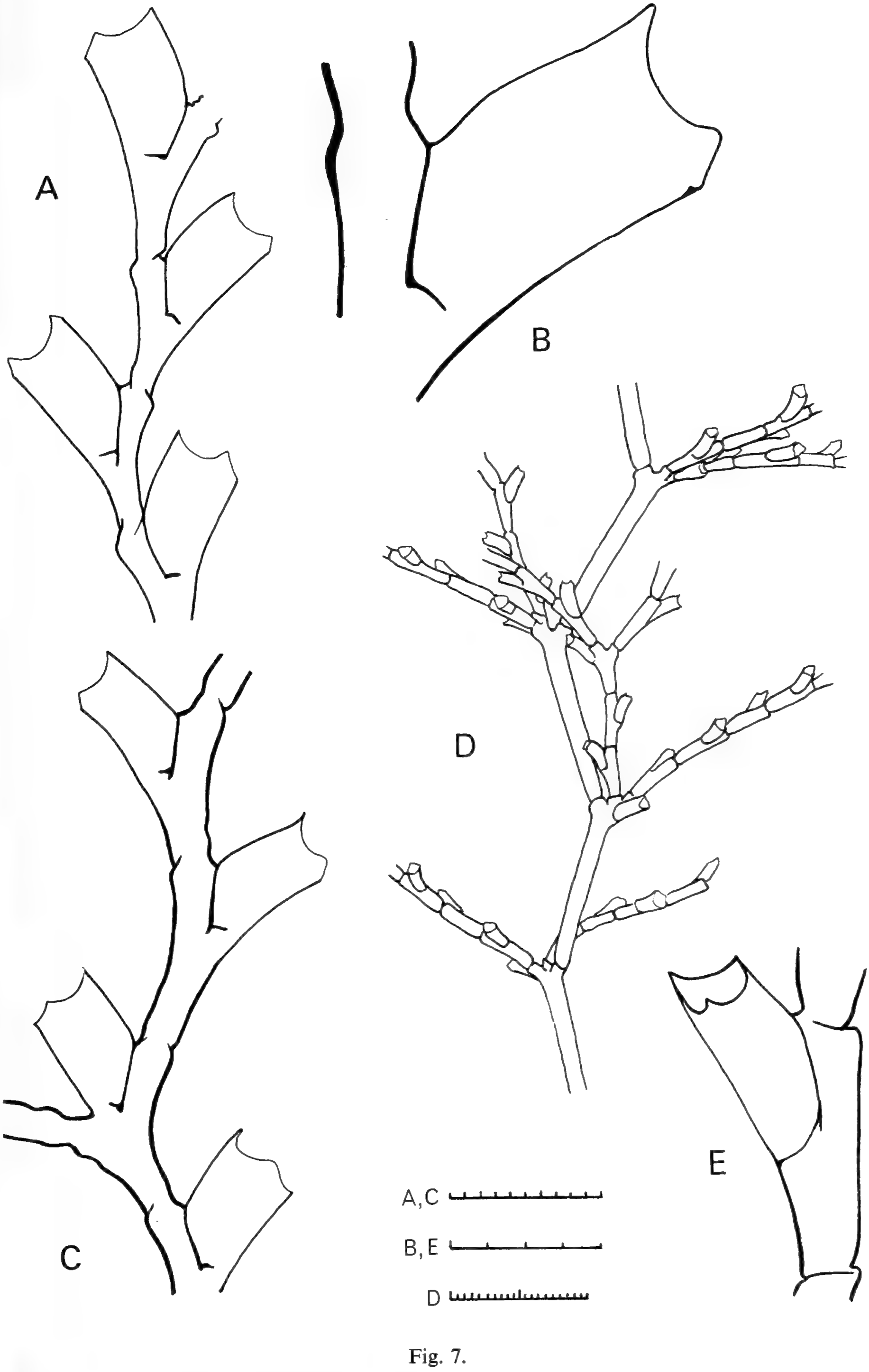

Fig. 7.

Symplectoscyphus curvatus (Jäderholm). A. Distal part of hydrocladium. B. Hydrotheca. C. Part of stem showing origin of hydrocladium.
Symplectoscyphus elongatus (Jäderholm). D. Part of stem showing origins of hydrocladia. E. Hydrotheca.

Scale in mm/10.

Measurements (mm)	26/64–C	*Symplectoscyphus exsertus* (Allman)
Internode length	0,80–1,32	0,43–0,60
Hydrotheca, length abcauline	0,62–0,70	0,28–0,32
length adcauline, adnate part	0,36–0,44	0,14–0,17
length adcauline, free part	0,59–0,68	0,22–0,28
adnate part/total adcauline length	0,35–0,41	0,35–0,44
diameter at mouth	0,41–0,49	0,12–0,14

Remarks

The measurements of the hydrothecae agree with those of Jäderholm and Totton; they are a little greater than those of Briggs and Naumov & Stepaniants.

S. curvatus shows resemblances to *S. exserta* (Allman, 1888) from Heard Island. However, the author has examined type material of the latter species and finds that it is much smaller in all its dimensions. The measurements are included above for comparison.

Symplectoscyphus elongatus (Jäderholm, 1904)

Figure 7D–E

Sertularia articulata Allman, 1888: 61, pl. 29 (figs 3, 3a).
Sertularella articulata: Jäderholm, 1905: 29, pl. 11 (fig. 4), pl. 12 (figs 1–3). Naumov & Stepaniants, 1972: 42, fig. 5A.
?*Sertularella spiralis* Hickson & Gravely, 1907: 19, pl. 3 (figs 19–20).
Sertularella elongata: Naumov & Stepaniants, 1962: 80, fig. 5. Naumov & Stepaniants, 1972: 42, fig. 5B.
Symplectoscyphus articulatus: Rees & Thursfield, 1965: 127.
Symplectoscyphus elongatus: Vervoort, 1972*a*: 136, figs 43, 44a (synonymy).

Stations

8/25–C; 26/64–D; 8/24–C.

Description

Three samples, the first with several infertile stems reaching 67 mm, the second with numerous infertile stems and fragments reaching a maximum height of 52 mm, and the third with numerous stems and fragments reaching a maximum height of 58 mm. None of the stems rooted. Stems golden brown in colour, unfascicled, geniculate. Internodes of stem very long, up to 3,3 mm, each bearing a prominent apophysis on distal end on which is seated one hydrotheca and on each side of it a hydrocladium, the apophyses with their paired hydrocladia arranged in a loose spiral. Nodes very distinct.

Hydrocladia bearing alternate hydrothecae, and commonly alternate sub-branches arising opposite every third hydrotheca, the two rows of hydrothecae and branches usually in one plane but occasionally very slightly displaced towards one surface. Internodes of variable length, those of hydrocladium bearing one or two hydrothecae, those of its sub-branches one.

Hydrothecae tubular, adnate for about half adcauline wall, abcauline wall straight or curved slightly outwards, with three prominent marginal teeth, but no internal teeth.

A few empty and damaged gonothecae present in 8/24–C, of the same shape and size as described by Hickson & Gravely (1907).

Measurements (mm)

Hydrotheca, length abcauline	0,39–0,52
length adcauline, adnate part	0,21–0,35
length adcauline, free part	0,18–0,36
adnate part/total adcauline length	0,37–0,65
diameter at mouth	0,17–0,23

Remarks

This species has been reported many times from Antarctic and Subantarctic waters; Kerguelen Island is the type locality. The synonymy of the species is fully discussed by Vervoort (1972*a*). This synonymy is accepted here, though with some reservations about the inclusion of *Sertularella spiralis* Hickson & Gravely, 1907, a form with internal hydrothecal teeth.

Symplectoscyphus mawsoni Briggs, 1939

Figures 8–9

Non Sertularella biformis Jäderholm, 1905: 28, pl. 11 (figs 1–3).
Sertularella biformis: Totton, 1930: 199, fig. 45, pl. 2 (fig. 8). Naumov & Stepaniants, 1972: 47, fig. 9.
Symplectoscyphus mawsoni E. A. Briggs, 1939: 35, fig. 2, pl. 16 (figs 1–2). Naumov & Stepaniants, 1972: 46, fig. 8.

Stations

10/30–A; 8/24–B.

Description

The first colony (10/30–A) consists of two stems 56 mm in maximum length, and a number of fragments. Basal part of stem lightly fascicled for 16–30 mm, the rest unfascicled and straight. Stem divided into internodes by distinct oblique nodes sloping in alternate directions. Each internode with a distal apophysis, alternately on the left and right, which bears a hydrotheca and two hydrocladia, one on each side of the hydrotheca, the two rows of hydrothecae in one plane. Many of the hydrocladia and hydrothecae of the lower half of the stem missing or damaged, those in the upper half better preserved. Each pair of hydrocladia forming an angle of about 40° with the stem and about 90° with each other. Hydrocladium divided into regular inter-

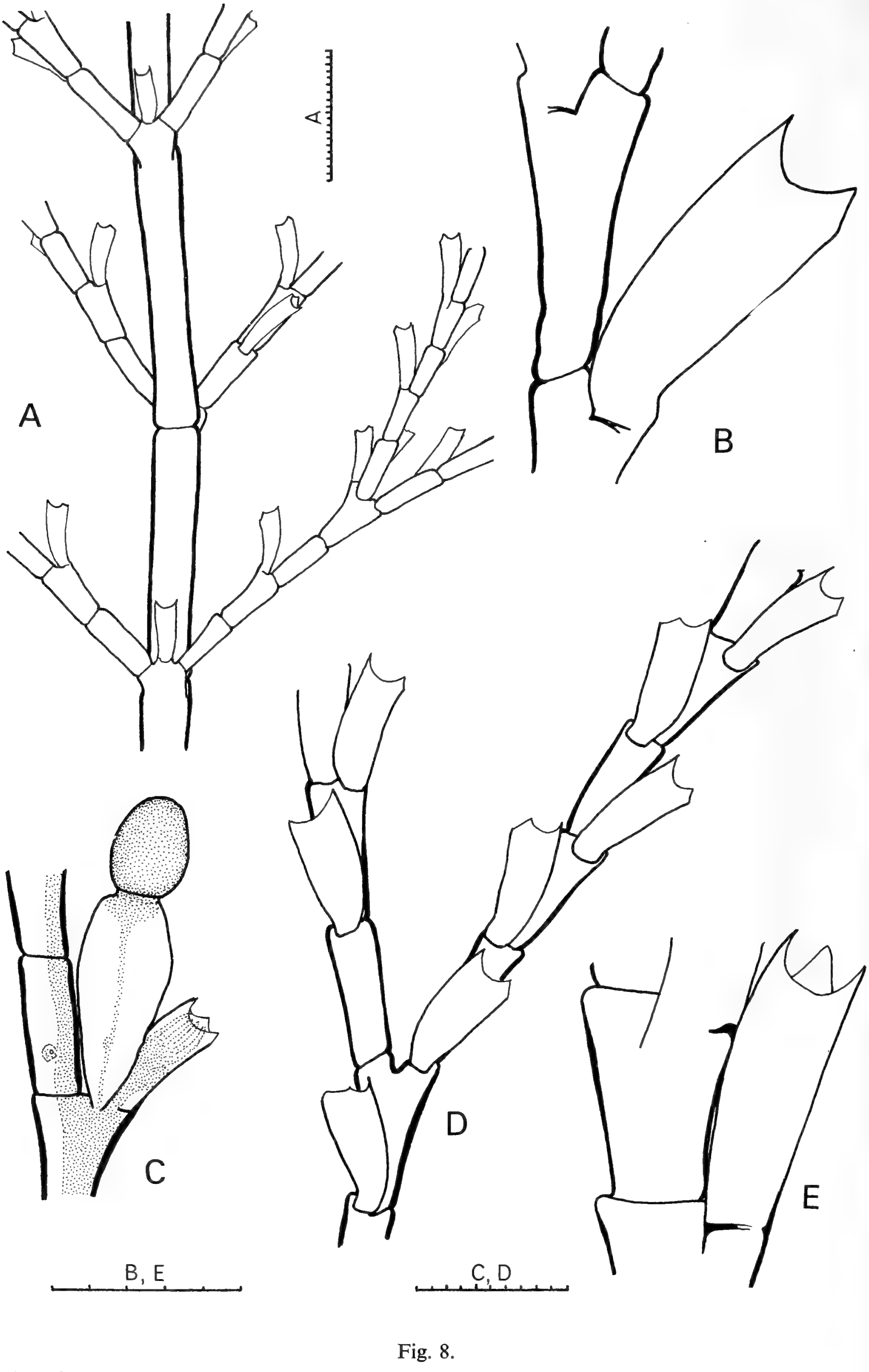

Fig. 8.

Symplectoscyphus mawsoni Briggs. A. Thick part of stem in side view showing origins of hydrocladia. B. Hydrotheca. C. Gonotheca with external marsupium. D. Part of hydrocladium showing bifurcation. E. A hydrotheca from Totton's material (BM 1929.10.28.158) attributed by him to *Sertularella biformis*, here included in *S. mawsoni*.

Scale in mm/10.

nodes by straight nodes, each bearing a hydrotheca near the distal end; dividing dichotomously at the distal end of the fourth internode, one limb of the dichotomy being slightly thicker than the other; both limbs sometimes dividing dichotomously once or twice more. The two rows of hydrothecae on the hydrocladium not in one plane but forming an acute angle between them. Hydrotheca completely free from internode, very delicate and often crumpled in basal part, curved outwards, widening towards aperture, with three well-developed marginal teeth, one adcauline and two latero-abcauline. No internal teeth. Operculum of three valves. Floor similar to that of *Sertularella* (Fig. 8A, B, D; Fig. 9 left).

The second colony (8/24–B) is in a very fragmentary condition, consisting mainly of small pieces of hydrocladia. There is, however, a stem of 110 mm with a few stumps of hydrocladia left; it is fascicled for the first 45 mm. Another portion of stem 46 mm long bears regular pairs of hydrocladia as in 10/30–A. The hydrocladia branch up to five times. This colony is fertile and bears

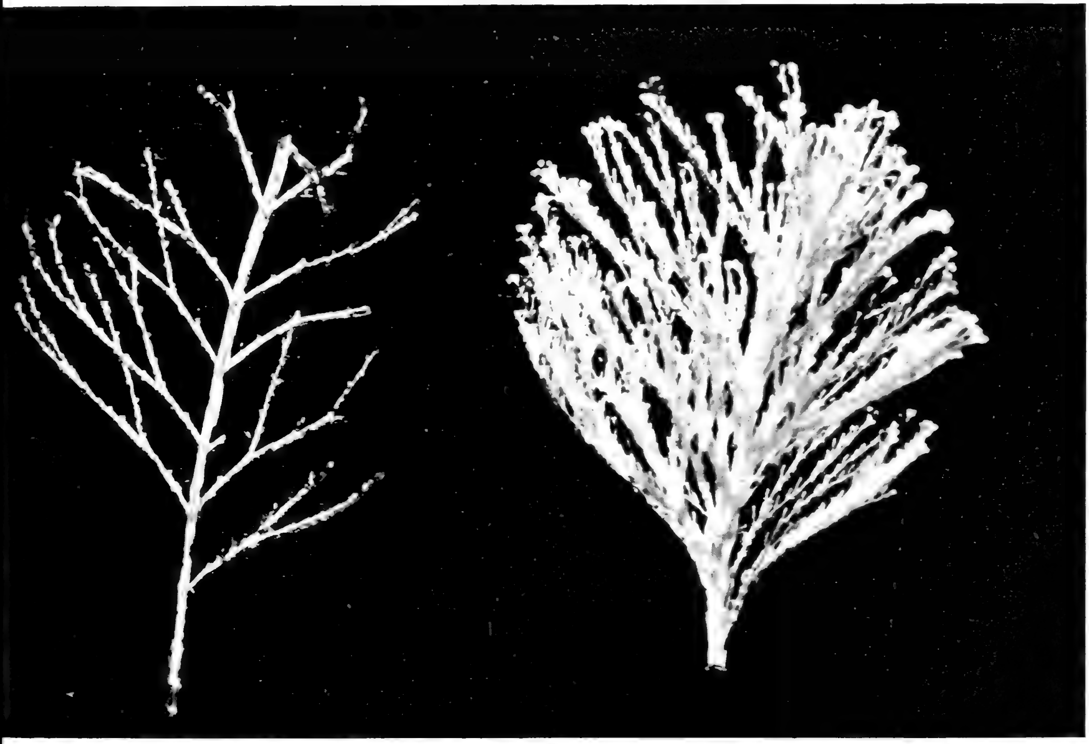

Fig. 9.

Symplectoscyphus mawsoni Briggs. A stem from the *Marion-Dufresne* collection (Station 10/30—A) on the left, compared with Totton's specimen attributed to *Sertularella biformis* on the right (× 2,5). Photo: D. Gerneke.

numerous gonothecae on the hydrocladial internodes. Female gonotheca elongated oboval, with external marsupium, containing one planula (Fig. 8C).

Measurements (mm)	10/30–A	8/24–B
Stem, internode length	2,20–3,95	2,50–4,10
diameter	0,52–0,70	0,50–0,62
Hydrocladium, internode length	0,57–1,09	0,67–1,15
Hydrotheca, depth abcauline	0,71–0,82	0,74–0,83
depth adcauline	0,87–1,00	0,92–1,01
diameter at margin	0,24–0,32	0,29–0,32

Remarks

Several species have been recorded from the Antarctic and Subantarctic which resemble one another in their method of branching, aptly described by Naumov & Stepaniants (1972) as 'panicle-shaped'. These can be divided into two groups:

1. Those where the hydrothecae are adnate for half or more of their height and where the 'panicle' is flexuous: included under the synonymy of *Symplectoscyphus elongatus* by Vervoort (1972*a*) and in this paper.
2. Those where the hydrothecae have little or no adnate part and where the 'panicle' is stiff.

It is the second group that concerns us here and it includes material recorded under the names of *Symplectoscyphus* (or *Sertularella*) *biformis* and *mawsoni*. Previous and present records of these species, together with the more important measurements, are listed in Table 1 (the depth of the hydrotheca is not included because of doubt as to exactly how it was measured by different authors).

The type material of *Sertularella biformis* Jäderholm, 1905, was examined (Fig. 10E–F), and Jäderholm's description is confirmed. The material differs from all other records in Table 1 in the absence of hydrocladia or any vestiges thereof, in the absence of nodes in most of the stem, in the grouping of the distal hydrothecae in three's, and in the shape of the hydrotheca which narrows towards the margin. Totton (1930) assigned material to this species (*S. biformis*) assuming that the specimens 'would correspond with the apical part missing from Jäderholm's type . . .', and that the stem progresses in complexity from base to apex, both assumptions being unwarranted. Totton's material, on examination, was found to differ from Jäderholm's in all the characters listed near the beginning of this paragraph (Fig. 8E, Fig. 9 right). It is clearly a different species altogether. Jäderholm's species has not been rediscovered to date, and the type material remains the sole specimen.

The remaining records in Table 1 seem to be conspecific and to form a series in the order shown, starting with the type material of *Symplectoscyphus mawsoni* Briggs and ending with Totton's material. In this series the complexity of branching in the hydrocladia increases, and the diameter of the hydrotheca

TABLE 1

A comparison of the Antarctic records of species of *Symplectoscyphus* of the *mawsoni* group. (Measurements to the nearest tenth of a mm.)

Species	Locality	No. of branches to hydrocladia	Stem inter-node length (mm)	Stem diameter (mm)	Hydro-cladium inter-node length (mm)	Marginal diameter of hydrotheca (mm)
Symplectoscyphus mawsoni Briggs, 1939 .	King George Land	0	−2,0		0,8	0,5
Sertularella mawsoni: Naum. & Step., 1972	Antarctic south of Australia	1	2,0–2,1		0,7–1,0	0,4–0,5
Marion-Dufresne material	Kerguelen Shelf	1–5	2,2–4,1	0,5–0,7	0,6–1,2	0,2–0,3
Sertularella biformis ?: Naum. & Step., 1972	Antarctic south of Australia	'rebranching repeatedly'	3,7–4,0	1,0	0,9–1,5	0,2–0,3
Sertularella biformis: Totton, 1930 . .	Cape Adare	3–4	1,1–2,5*	0,9–1,0*	0,5–0,8*	0,2–0,3*
Sertularella biformis Jäderholm, 1905 . .	Graham Land	No hydrocladia	No nodes	0,1–0,4*	—	0,2*

* Supplemented by author's own measurements.

decreases. The stem internodes increase in length except for Totton's material where they are relatively short and wide so that the hydrocladia are closer together and give a dense 'bottle-brush' appearance to the colony. The material of Naumov & Stepaniants (1972) attributed with a query to *Sertularella biformis* differs from the rest in the absence of hydrothecae on the stem, but it is very possible that these have been damaged or eroded away. (Totton omitted to state that his material possesses cauline hydrothecae.)

The present material from the Kerguelen area lies about mid-way in the series resembling Briggs' material in the appearance of the colony and the structure of the stem internodes, but resembling Totton's material in the shape of the hydrothecae.

It seems that the first five samples in Table 1 cannot be separated on any definite characters and it is proposed to unite them under the name *Symplectoscyphus mawsoni* Briggs, 1939. The gonothecae were first described by Naumov & Stepaniants (1972, fig. 9).

Symplectoscyphus plectilis (Hickson & Gravely, 1907)

Figure 11A–C

Sertularella plectilis Hickson & Gravely, 1907: 20, pl. 3 (fig. 21). Ritchie, 1913: 30, figs 8, 9, 11. Broch, 1948: 11, fig. 2f–g.
Symplectoscyphus plectilis: Vervoort, 1972*b*: 354, fig. 8b–c.

Station

14/44–C.

Description

A single, small infertile colony of about 12 stems growing on *Halecium* sp. Stem unfascicled, reaching a maximum height of 9 mm, slender, slightly geniculate, branching sparingly and in one plane. Branches arising from apophyses immediately below hydrothecae at a wide angle (95–125°). Nodes usually indicated by indentations of perisarc only. The two rows of hydrothecae in one plane.

Hydrotheca very small, tubular, curved outwards, adnate for about one-third adcauline length, narrowing to margin. Marginal teeth well developed. No internal teeth.

Measurements (mm)

Internode, length	0,39–0,63
Hydrotheca, length abcauline	0,23–0,29
length adcauline, adnate part	0,09–0,14
length adcauline, free part	0,22–0,28
adnate part/total adcauline length	0,26–0,36
diameter at margin	0,08–0,12

Remarks

The hydrothecae in this material are of a similar size to those described by Ritchie (1913); they are a little longer than those described by most other authorities.

S. plectilis is known from a number of localities in the Antarctic and Subantarctic, the nearest to the present locality being Bouvet Island (Broch 1948). The distribution and synonymy are summarized by Vervoort (1972*b*).

Symplectoscyphus subarticulatus (Coughtrey, 1875)

Figure 10A–D

Thuiaria sub-articulata Coughtrey, 1875: 287, pl. 20 (figs 32–34).
Symplectoscyphus subarticulatus: Ralph, 1961: 801, 811, figs 14g–h, 15a–c (synonymy). Blanco, 1968: 213, pl. 4 (figs 1–3). Leloup, 1974: 41, fig. 38.

Stations

2/6–B (fertile); 2/7–A; 14/45–C.

Description

Fascicled, pinnate stems reaching a maximum height of 105 mm and a maximum diameter at the base of 1,5 mm. Hydrothecae completely obscured by the peripheral tubes in the proximal part of the stem, with only the margins visible in the central region, uncovered in the distal unfascicled region. In the distal region nodes fairly clearly marked and sloping in alternate directions, each internode bearing three hydrothecae and a hydrocladium arising immediately below the third hydrotheca. The two rows of hydrothecae and hydrocladia in one plane.

Hydrocladium separated from stem apophysis by a distinct node, narrower than stem. Nodes scarce, oblique, not well marked, sometimes not visible for the entire length. Hydrothecae closely set, more so in the distal region where the margin of one overlaps the base of the next, most hydrothecae with a fenestra immediately below the base on one side.

Hydrotheca tubular, curved outwards, adnate for about two-thirds adcauline height.

Gonothecae borne on hydrocladia below hydrothecae, long and carrot-shaped, widest at distal end, strongly annulated with 15–17 circular crests (not spiral), with terminal aperture on a raised collar.

Measurements (mm)

Hydrotheca, length abcauline	0,40–0,47
length adcauline, adnate part	0,38–0,60
length adcauline, free part	0,23–0,31
adnate part/total adcauline length	0,57–0,70
diameter at margin	0,31–0,33
Gonotheca, length	2,35–3,10
maximum diameter	0,86–1,24

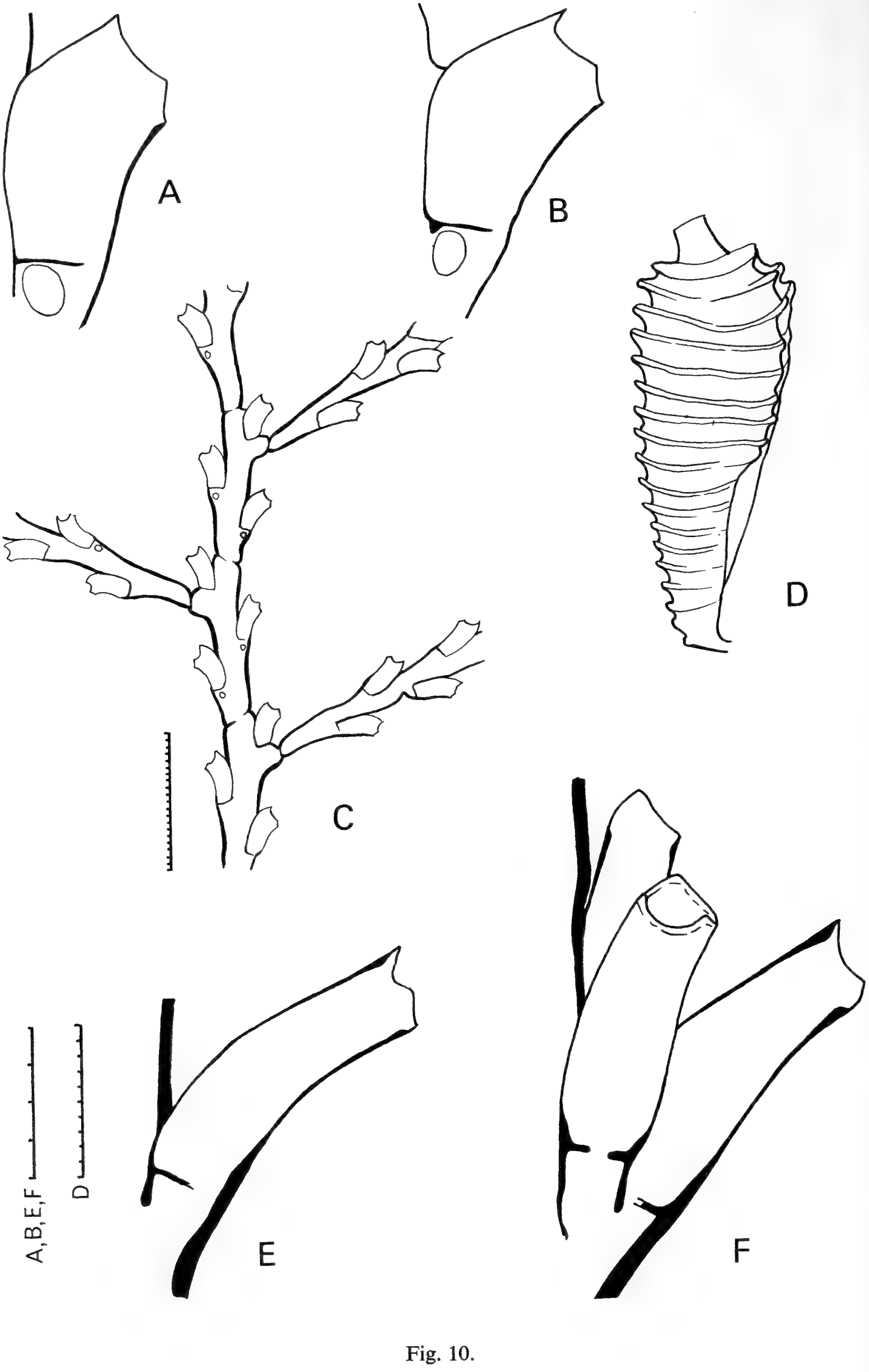

Fig. 10.

Symplectoscyphus subarticulatus (Coughtrey). A–B. Hydrothecae. C. Distal part of stem showing origins of hydrocladia. D. Gonotheca.
Symplectoscyphus biformis (Jäderholm). E. A single hydrotheca. F. A group of three hydrothecae. Drawn from the holotype.

Scale in mm/10.

Remarks

The hydrothecae of this material are larger than those of Ralph but smaller than those of Blanco. The details of structure and the method of branching agree exactly with those described by Ralph. The only hesitation in the identification lies in the gonotheca, which is about twice the length of that described by Ralph and has more annulations (15–17 as against 5–8). However, the shape of the gonotheca is exactly like that depicted by Coughtrey (he does not give the size, but the diagram shows 10 annulations).

S. subarticulatus is best known from New Zealand, but recent reports show that it also occurs in the southern Argentine (Blanco) and in Chile (Leloup). It is a new record from the Kerguelen area.

Symplectoscyphus subdichotomus (Kirchenpauer, 1884)

Figure 11D–F

Sertularella subdichotoma Kirchenpauer, 1884: 46, pl. 16 (fig. 1).
Symplectoscyphus subdichotomus: Blanco, 1969: 49, figs 1–18. Vervoort, 1972*a*: 140, figs 44b–d, 45 (synonymy). Leloup, 1974: 42, fig. 40.

Stations

Small form: 8/25–E; 26/64–E (fertile); 26/65–A (fertile); 28/71–C (fertile); 30/73–D; 31/74–G.

Large form: 3/11–D; 14/44–B; 21/57–D; 22/58–J; 26/63–F.

Description

Colonies flexuous and straggling, growing profusely with polyzoans and *Sertularella picta*, and often intertwined to form a bushy mat. Stem unfascicled, reaching 33 mm in height (small form) or 58 mm (large form), generally geniculate and giving off a branch at each elbow immediately below every third hydrotheca, but many irregularities present. The two rows of hydrothecae and branches in one plane. Branches of same diameter as stem, forming an angle of 85–108° with it, and often rebranching producing a subdichotomous effect. Most of the nodes not clearly defined and recognizable only by an indentation of the perisarc, but those at the origin of each branch, and on the stem immediately above each axillary hydrotheca, more clearly defined and usually forming a definite septum. Internodes always longer than the hydrothecae, which do not overlap each other.

Hydrotheca adnate for over half adcauline height, curved outwards, widest in centre and narrowing to margin, with three well-developed marginal teeth and no internal teeth.

Gonotheca obovate (female), with 10–11 strong and crested circular annulations (not spiral) and a long flaring mouth-funnel, containing two or three large planulae.

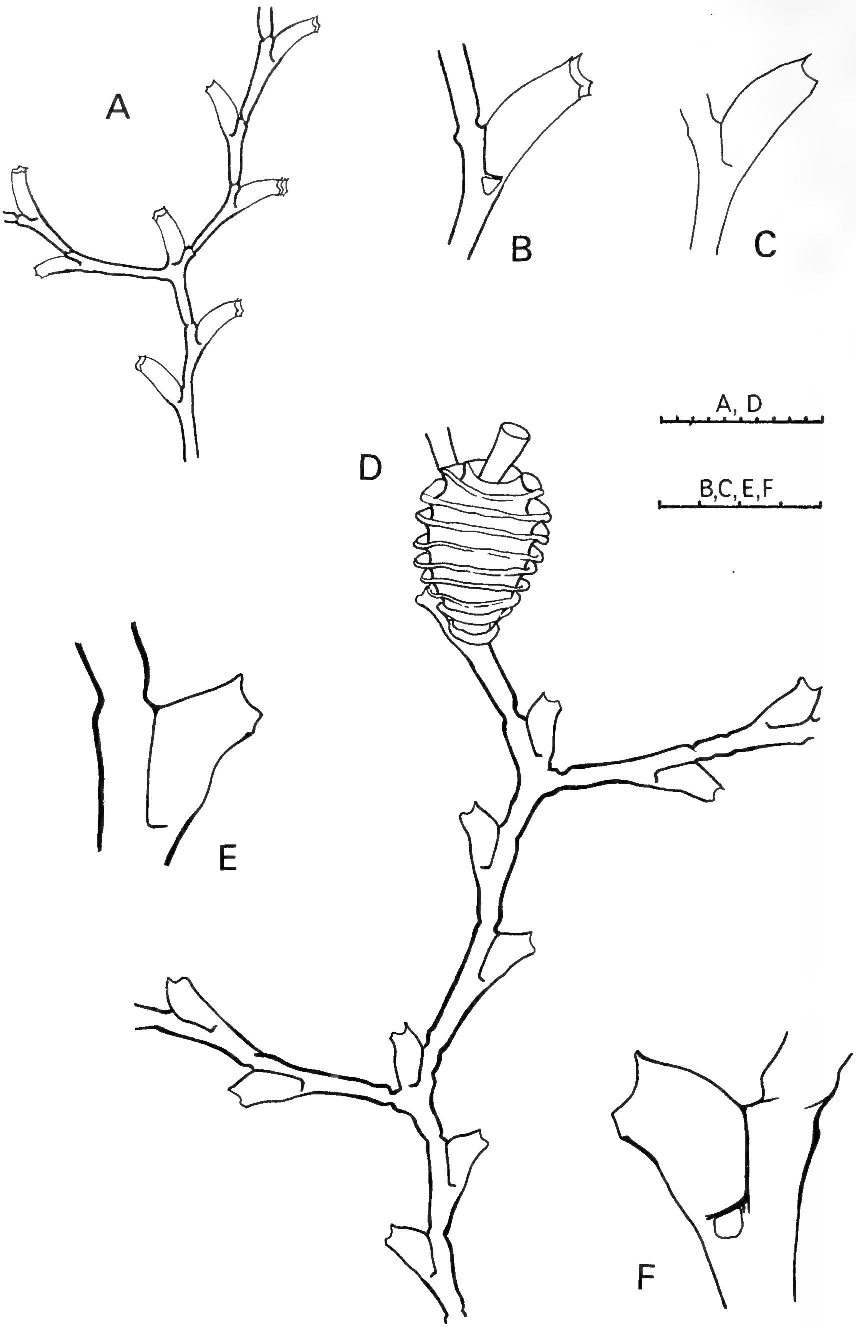

Fig. 11.

Symplectoscyphus plectilis (Hickson & Gravely). A. Part of stem showing origin of hydrocladium. B–C. Hydrothecae.
Symplectoscyphus subdichotomus (Kirchenpauer). D. Stem of small form showing origins of hydrocladia and a gonotheca. E. Hydrotheca of small form. F. Hydrotheca of large form.

Scale in mm/10.

Measurements (mm)

	Small form	*Large form*
Internode length	0,47–0,74	0,74–1,27
Hydrotheca, length abcauline	0,26–0,31	0,28–0,38
length adcauline, adnate part	0,25–0,30	0,25–0,39
length adcauline, free part	0,13–0,21	0,14–0,28
adnate part/total adcauline length	0,58–0,68	0,48–0,71
diameter at mouth	0,13–0,17	0,20–0,30
Gonotheca, length	1,06–1,55	
maximum diameter	0,58–0,84	

Remarks

As far as the detailed measurements are concerned this material includes two size-ranges—a small and a large—the smaller fitting best with the dimensions given by Vervoort, Blanco and earlier workers. The growth-form and structure of the two are the same, but there are no gonothecae to confirm the identification of the larger form.

The synonymy of *S. subdichotomus* has been reviewed by Vervoort (1972*a*), who also gave some excellent diagrams. There is no doubt at all that the present material (at any rate the smaller form) belongs to the same species. Because of the presence of a number of closely allied species of dubious validity, the geographical range is uncertain—the species is certainly common in the Falklands/South American region, but has apparently not been reported from Kerguelen.

Family **Plumulariidae**

Kirchenpaueria triangulata (Totton, 1930)

Plumularia triangulata Totton, 1930: 225, fig. 61.
Kirchenpaueria triangulata: Millard, 1975: 375, fig. 119E–H.

Station

17/50–B.

Description

A rich, fertile colony epizootic on *Plumularia insignis*. Stems reaching 18 mm in height, unfascicled, with nodes absent or very indistinct, otherwise details as in previous descriptions. Gonophores female, reaching 2 mm in length, triangular in section and containing a single layer of eggs over a central spadix.

Remarks and distribution

This is a new record for the Kerguelen area. The species was previously known from South Africa (in depths greater than 100 m) and from New Zealand.

Oswaldella bifurca (Hartlaub, 1904)

Figure 12A–C

Schizotricha bifurca Hartlaub, 1904: 16, pl. 3 (figs 4–8).
Oswaldella bifurca: Totton, 1930: 208, fig. 50. Naumov & Stepaniants, 1962: 98.

Station

26/64–J.

Description

Several infertile stems reaching a maximum height of 22 mm. Stem divided by transverse nodes into internodes which usually bear one hydrocladium each, but rarely two. Cauline nematothecae very difficult to distinguish and sometimes missing; at the maximum development there is one mamelon on the hydrocladial apophysis and one nematotheca in the axil, with another nematotheca (or a naked sarcophore) on the main stem above the axil.

Hydrocladia unbranched near the proximal and distal ends of colony, branched in the central region. Branches arising from below hydrothecae and to one side, as many as four from one hydrocladium, and these may be all on the same side, on alternate sides or in opposite pairs. One secondary hydrocladium has a tertiary branch.

The two rows of primary hydrocladia not in the same plane but displaced towards anterior surface of stem. Secondary hydrocladia similarly displaced, so that the whole arrangement is in at least six different planes and presents a stiff and spiky appearance. Since the hydrothecae are borne on the anterior surface of the hydrocladia, those of primary and secondary hydrocladia do not face one another.

Hydrocladia generally heteromerous with alternating athecate and thecate internodes, but many variations; the athecate internodes may be absent or duplicated, long or short, and may or may not bear a median nematotheca. Thecate internodes usually with one median inferior and one median superior nematotheca, but the nematotheca is often missing leaving only a naked sarcophore, and this is especially common in the first thecate internode of the hydrocladium. Nematothecae, when present, curved and scoop-shaped. Median superior nematotheca situated behind distal part of adcauline thecal wall which is not completely adnate.

Hydrotheca wider than deep, with more or less straight abcauline wall and margin at least slightly oblique.

Measurements (mm)

Thecate internode, length	0,42–0,96
Hydrotheca, depth abcauline	0,12–0,19
diameter at margin	0,17–0,22

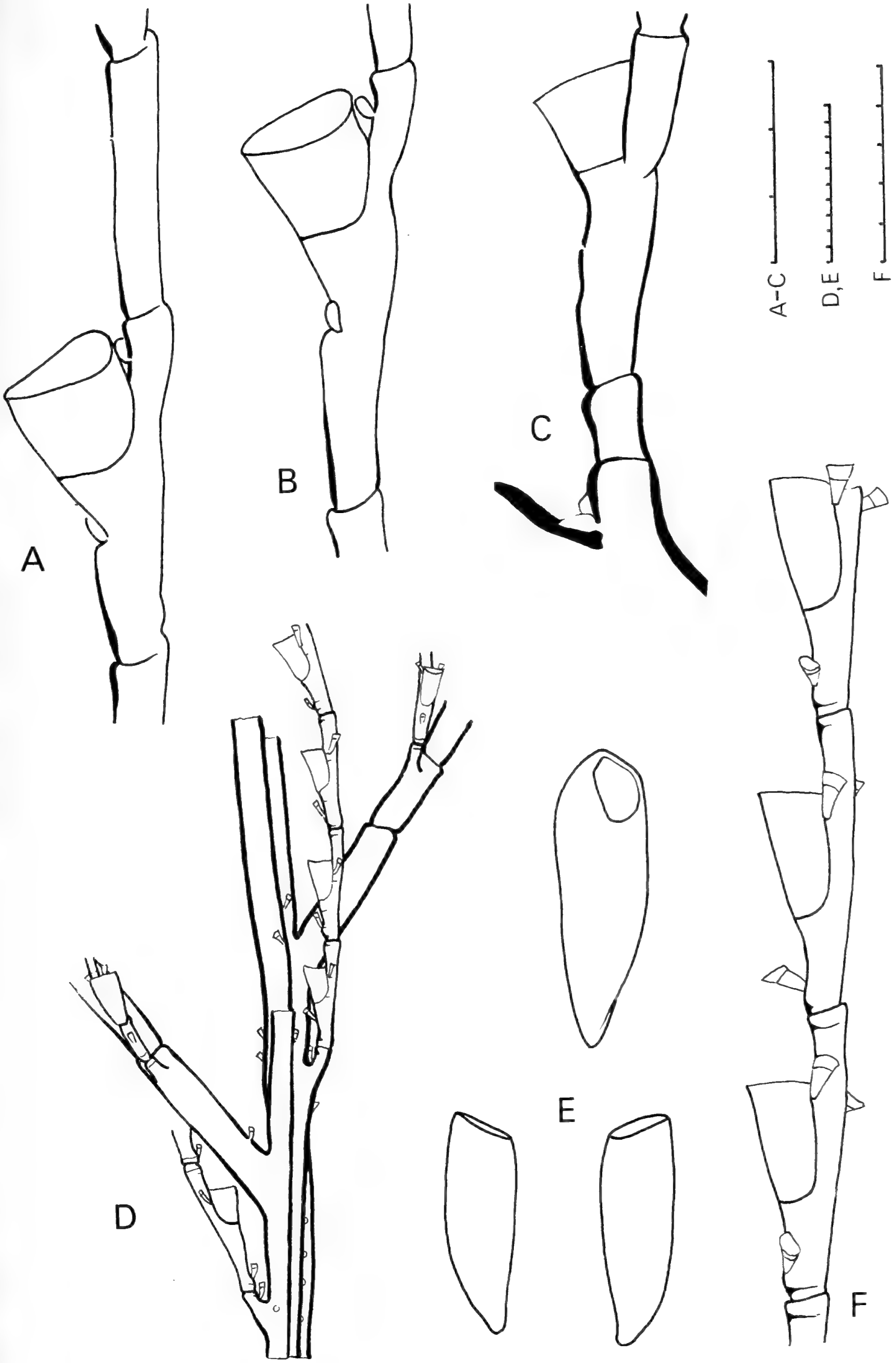

Fig. 12.

Oswaldella bifurca (Hartlaub). A–B. Normal parts of hydrocladia. C. Proximal end of hydrocladium showing origin from stem and first thecate internode which is without a nematotheca.
Plumularia insignis Allman. D. Part of stem in thinner region showing origins of two branches and their preceding hydrocladia. E. Gonothecae. F. Part of hydrocladium.

Scale in mm/10.

Remarks

This material is assigned to *O. bifurca* with some hesitance, the decision being based mainly on the shape of the hydrotheca, which is wider than deep, and on the method of branching. As regards the latter feature Totton's words (1930) are pertinent, when he says for *O. bifurca* 'Hydrothecae of hydroclade and branch not strictly opposed, but facing slightly upwards'. On the other hand the features used by Totton as diagnostic for *O. bifurca*, namely 'once-branched hydrocladia' and the absence of an inferior nematotheca on the first hydrocladial internode, are found to be variable and of dubious value. The presence of athecate internodes in the hydrocladium and the number of hydrocladia to a stem internode are also variable characters. This species is known from various localities in the Antarctic; it has not been reported before from Kerguelen.

Plumularia insignis Allman, 1883

Figure 12D–F

*Plumularia flabellum** Allman, 1883: 19, pl. 1 (figs 1–4).
Plumularia insignis Allman, 1883: 21, pl. 2. Billard, 1910: 32, fig. 14.
Plumularia abietina Allman, 1883: 21, pl. 3.
Plumularia insignis v. *flabellum:* Billard, 1910: 34, fig. 15.
Plumularia insignis v. *abietina:* Billard, 1910: 35.
Plumularia sp. Naumov & Stepaniants, 1962: 99, fig. 19.

Stations

3/10–A; 3/11–C; 7/22–A; 17/50–A; 18/52–A; 23/59–D; 24/61–A; 26/64–A; 30/73–E.

Description

Many magnificent colonies, the tallest reaching 940 mm. Rootstock a mass of interwoven fibres suitable for anchoring in mud. Stem long, flexuous or fairly stiff, fascicled for the greater part, giving off branches in all planes, unsegmented. Immediately below each branch a single hydrocladium arises from the stem and from the same component tube, otherwise cauline hydrocladia occur only rarely. Component tubes of stem bearing longitudinal rows of nematothecae.

Branches fascicled or unfascicled, pinnate, divided by transverse nodes at irregular intervals into internodes bearing one to four alternate hydrocladia. Hydrocladial apophysis with two axillary nematothecae (one anterior and one posterior) with a mamelon between them, and one (or rarely two) nematothecae on distal end. Nematothecae on main axis rather irregular, but at least one between every two successive hydrocladia and several below the first hydrocladium.

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* Although *P. flabellum* has page priority over *P. insignis*, from Article 24(a) of the Code of Zoological Nomenclature, Billard (1908: 759) counts as the 'first reviser' and he has clearly chosen *P. insignis* as the name of the composite species.

In some colonies the hydrocladia bear practically only thecate internodes, each with one hydrotheca and three nematothecae (one median inferior and one pair of laterals), athecate internodes occurring only sporadically and obviously resulting from regeneration after injury. In other colonies intermediate athecate internodes are present throughout, each with one median nematotheca and two internodal septa. Thecate internodes very rarely have two median inferior nematothecae. Internodal septa usually not so well developed as in the type material: 1–2 below hydrotheca, 0–3 behind it, and 0–1 above it.

Gonothecae arising from branches next to hydrocladia, elongated, widening distally, with a terminal oblique opening, as illustrated by Allman (1883) for *P. abietina.*

Measurements (mm)

Thecate internode, length	0,54–0,80
Hydrotheca, height abcauline	0,21–0,34
diameter at margin	0,14–0,21
Gonotheca, length	1,40–1,95
maximum diameter	0,35–0,58

Remarks

This species occurs in several varieties, of which three (described by Allman as *P. insignis*, *P. flabellum* and *P. abietina*) are known from the Subantarctic. In the general appearance of the colony and in the detailed measurements, most of the present material closely resembles the nominal variety illustrated by Allman (1883: pl. 2). One colony, however (26/64–A), is of stouter build and more irregular branching and is more like Allman's diagram of *P. flabellum* (1883: pl. 1). Of the three, Allman showed hydrocladia on the main stem only in *P. flabellum*, Nowhere has the singular character of one hydrocladium below each branch been described, and if this character is indeed peculiar to the Kerguelen material it would be worth naming a separate variety.

Most of this material is unusual in possessing as the 'normal' condition only thecate internodes in the hydrocladia, athecate internodes being rare and sporadic. One colony alone (26/64–A, mentioned also above) has regular intermediate athecate internodes. Billard (1910) has commented on the irregularity of occurrence of athecate internodes which are often the result of regeneration after injury. Naumov & Stepaniants (1962) described some infertile material from Kerguelen and Heard Islands without athecate internodes as *Plumularia* sp. This is without doubt the same species.

The species is known from Prince Edward Island, Marion Island, Kerguelen and Heard Islands, and there are two varieties from the East Indies.

Schizotricha unifurcata Allman, 1883

Schizotricha unifurcata Allman, 1883: 28, pl. 7 (figs 1–3). Stechow, 1925: 498. Totton, 1930: 231, fig. 65, pl. 3 (fig. 4). Naumov & Stepaniants, 1972: 54. Blanco & De Miralles, 1972: 21, pl. 5 (figs 34–40).

Polyplumaria unifurcata: Billard, 1910: 41, fig. 18.

Stations

8/25–A; 9/26–B (fragments); 10/30–B; 22/58–A; 23/59–C.

Description

Stems with tangled rootstock for mud-penetration and reaching 175 mm in height. Hydrocladia branching one to three times, 10–18 mm in length. Details of hydrocladia as in type material.

Male gonothecae present on first colony, arising from thecate internodes below hydrothecae, pear-shaped, with oblique distal aperture, bearing two to four nematothecae on basal region.

Remarks

Stechow (1925) combined the species *S. unifurcata* Allman, 1883; *S. turqueti* Billard, 1906; *S. anderssoni* Jäderholm, 1904; and *S. glacialis* (Hickson & Gravely, 1907) under one name. Totton (1930) added *S. multifurcata* Allman, 1883. All of these species are Antarctic or Subantarctic in distribution.

This material is very similar to the type material and indeed, two of the colonies come from the type locality (Kerguelen Island).

DISCUSSION

Of the 33 species here recorded (omitting *Campanularia* sp.) 5 are cosmopolitan, namely *Modeeria rotunda*, *Halecium delicatulum*, *Halecium tenellum*, *Filellum serratum* and *Lafoea dumosa* (Table 2).

The remaining 28 species show only a very slight affinity with the nearest continental masses, for only 1 (3,6%) also occurs in South Africa (*Kirchenpaueria triangulata*) and only 8 (28,6%) also occur in the Australasian region.

The affinities of these 28 species are in fact mainly with the South American region (or Magellan Province, including the Falklands and South Georgia) and with the Antarctic Continent, for 19 of the species (67,9%) also occur in the former and 14 (50,0%) in the latter.

Surprisingly, there is little obvious affinity with Bouvet Island (3 species: 10,7%) or Marion and Prince Edward Islands (5 species: 17,9%) which lie at much the same latitude, but this is probably merely a reflection of the inadequate knowledge of these islands.

This analysis thus supports the classification of the Kerguelen and Crozet groups of islands as Subantarctic (J. C. Briggs 1974), with a fauna intermediate between that of the Cold Temperate South American Region and the Antarctic Region. As has been remarked by Naumov & Stepaniants (1962), it is not possible to draw a sharp line of demarcation between the fauna of the Antarctic and that of the Subantarctic.

There is at this stage a little evidence of a divergence between the fauna of the Kerguelen group on the one hand and the Crozet group on the other. Although they share 12 (42,9%) of the non-cosmopolitan species, 8 occur only in Kerguelen and 8 only in Crozet.

TABLE 2
The distribution of the 33 species recorded in this paper.

	Crozet group	Kerguelen group	Magellan region	Bouvet Island	Marion & Prince Edward	Macquarie	Antarctica	South Africa	New Zealand/Australia	
Eudendrium rameum	×	×	×							
E. tottoni		×	×				×			
Modeeria rotunda	×	×	×					×	×	(cosmop.)
Opercularella belgicae		×	×				×			
Phialella chilensis	×		×						×	
Halecium delicatulum	×	×	×		×	×	×	×	×	(cosmop.)
H. dufresneae	×									
H. jaederholmi	×		×				×			
H. tenellum		×	×				×	×	×	(cosmop.)
Hydrodendron arborea	×	×	×		×		×			
Filellum serratum	×	×	×					×	×	(cosmop.)
Grammaria abietina	×	×	×							
Halisiphonia ?nana	×			×						
Hebella striata	×	×	×				×			
Lafoea dumosa		×	×			×	×	×	×	(cosmop.)
Zygophylax crozetensis	×	×								
Campanularia norvegiae		×	×							
Silicularia rosea	×	×	×		×	×			×	
Tulpa diverticulata	×	×							×	
Staurotheca antarctica	×		×				×		×	
S. dichotoma	×	×	×		×		×			
Sertularella geodiae	×		×						×	
S. picta	×	×	×		×					
Symplectocyphus curvatus	×						×			
S. elongatus	×	×	×				×			
S. mawsoni		×					×			
S. plectilis		×	×	×			×			
S. subarticulatus		×	×						×	
S. subdichotomus	×	×	×				×		×	
Kirchenpaueria triangulata		×						×	×	
Oswaldella bifurca	×						×			
Plumularia insignis	×	×			×					
Schizotricha unifurcata		×	×	×			×			
Total (less cosmop.)	20	19	19	3	5	1	14	1	8	
% (less cosmop.)	71,4	67,9	67,9	10,7	17,9	3,6	50,0	3,6	28,6	

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The British Museum (Natural History) granted permission for the examination of *Challenger* material of *Sertularia* (*Symplectoscyphus*) *exserta* and *Terra Nova* material of '*Sertularella biformis*', while the Naturhistoriska Riksmuseum, Stockholm, permitted examination of type material of *Sertularella biformis* from the Swedish Southpolar Expedition. This help is gratefully acknowledged.

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Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

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Family **Nuculanidae**

Nuculana (*Lembulus*) *bicuspidata* (Gould, 1845)

Figs 14–15A

Nucula (*Leda*) *bicuspidata* Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (figs 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

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In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33°51′S 25°39′E), collected by A. Smith, 15 January 1973.

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Fischer, P.-H. 1948. Données sur la résistance et de le vitalité des mollusques. *J. Conch., Paris* **88**: 100–140.
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(continued inside back cover)

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RELATIONSHIPS OF THE SOUTH AFRICAN FOSSIL FROG *EOXENOPOIDES REUNINGI* (ANURA, PIPIDAE)

By

RICHARD ESTES

Department of Zoology, San Diego State University,
San Diego, California

(With 11 figures)

[*MS. accepted 29 December 1976*]

ABSTRACT

The relationships of the South African fossil frog, *Eoxenopoides reuningi*, originally described as a pipid, have been questioned and several authors have placed it in a separate family Eoxenopoididae. Restudy of the original material for the first time since its original description shows this frog to be, in fact, a pipid as originally described and to have a remarkable mixture of primitive and derived character states. The anterior position of parietal foramen, scapula length, unfused carpus and expanded transverse processes of posterior vertebrae indicate *E. reuningi* as more primitive than any living pipid. Highly specialized in lacking teeth, and particularly in reduction and fusion in the vertebral column that results in possession of only six presacral vertebrae, it has nevertheless only one derived character state in common with the extant specialized *Hymenochirus* and South American pipids. Its greatest number of derived character states are in common with species of the living pipid *Xenopus*, but there is no indication of greater proximity to any one of them and *E. reuningi* appears to have diverged from the ancestor of the living genus some time prior to the late Cretaceous.

Review of available radiometric and palaeontological evidence suggests a Palaeogene age (perhaps late Eocene or Oligocene) for *Eoxenopoides reuningi* rather than the original suggestion of late Cretaceous or early Tertiary.

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INTRODUCTION

Large collections of fossil frogs are rare. One such collection, made in the early 1930s first by E. Reuning and later by L. Boonstra in Namaqualand, north-western South Africa, has received little attention since its original description (Haughton 1931). Over the last several years, the author has been concerned with

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the fossil record of pipid frogs, and need for revaluation of this important collection was seen through comparisons made during study of fossil *Xenopus* from Brazil (Estes 1975*a*, 1975*b*).

Haughton referred all the frogs in the collection to a single genus and species *Eoxenopoides reuningi*, and he prepared a careful description of his material. Most of the fossil pipid frogs (indeed most fossil frogs in general) have been described since that time, and Haughton was thus unable to evaluate his material as thoroughly as it is possible to do now. The most recent summary of the frog fossil record is given by Estes & Reig (1973), and a further evaluation of fossil pipids may be found in Estes (1975*a*); only such literature and discussion as is pertinent to the revaluation of *Eoxenopoides* will be repeated here.

Although Haughton's description was carefully done, his drawings were somewhat diagrammatic and the nature of the material led to some misinterpretation of bones. It is no surprise, therefore, that the very little written about the genus subsequent to Haughton's account is incorrect for the most part and has confused rather than clarified the status of the animal; so far as the author is aware no one of these subsequent papers has been based on personal observation of the fossil material.

Kuhn (1941) cited it as belonging to a 'fam. opisthocoelorum nov.', and as 'recht aberrante Opisthocoelia . . .'. He did not at that time name a new family, but suggested relationships with his middle Eocene genus *Opisthocoelellus* from Germany. Reig (1958), in discussing a proposed new classification of frogs, noted that *Eoxenopoides* 'pertenece a una familia seguramente nueva, que también debe relacionarse estrechamente con la de los pipidos', but gave no explanation as to why a new family was suggested. Shortly after this, Casamiquela (1960, 1961) described the frog *Shelania pascuali* from the Eocene of Patagonia, giving presumed resemblances between *Eoxenopoides* and *Shelania*; he used these resemblances in 1961 to define a new family Eoxenopoididae to include the two genera, and suggested a more primitive but close relationship to Pipidae. He was unaware, apparently, that the family name Eoxenopoididae had already been used the previous year by Parodi Bustos *et al.* (1960), who referred late Cretaceous frogs from northern Argentina to a new species *Eoxenopoides*? *saltensis*. The name *Saltenia ibanezi* had already been applied to this taxon by Reig (1959), based on fossils from the same locality; Reig referred *S. ibanezi* to the Aglossa. Parodi Bustos *et al.* seemed not to have been aware of Reig's paper initially, but after receiving it Parodi Bustos & Kraglievich (1960) defended with additional force their generic identification, stating that 'el material . . . no puede separarse genericamente de *Eoxenopoides*'. Later, Parodi Bustos (1962) agreed with Casamiquela (1961) that *Shelania pascuali*, *Eoxenopoides*? *saltensis* and *E. reuningi* belonged to the same family. Meanwhile, however, Kuhn (1961) had also named a new family Eoxenopoididae, including only *Eoxenopoides reuningi*. He apparently had not seen the papers of Parodi Bustos but suggested that *Saltenia ibanezi* Reig belonged to yet another new family, which he did not name. The family Eoxenopoididae was thus named independently three times, by Parodi

Bustos *et al.* (1960), by Casamiquela (1961) and by Kuhn (1961). Hecht (1963) mentioned *Eoxenopoides* as constituting evidence for wide distribution of the Aglossa during the Cretaceous (in combination with other aglossan fossils) but made no taxonomic judgements.

Nevo (1968) was the first to attempt clarification of this issue. He correctly pointed out that the character states used by Casamiquela (1961) to set up the family Eoxenopoididae were 'inappropriate as taxonomic criteria at the family level'. He returned *Eoxenopoides reuningi* to the Pipidae, following the original decision made by Haughton in 1931; this allocation is supported and documented in the present paper. Current work on *Shelania* cited by Estes (1975*a*) has shown it to be congeneric with *Xenopus* and hence a pipid as well (Báez & Estes in preparation). Báez (in ms. as noted by Estes & Reig 1973, and Estes 1975*a*) has confirmed that *Eoxenopoides*? *saltensis* Parodi Bustos *et al.* is a junior synonym of *Saltenia ibanezi* Reig, and that the taxon is unquestionably referable to the Pipidae. As the present study and that of Báez demonstrates, *Saltenia* and *Eoxenopoides* are not closely related, although both are pipids.

It will be attempted to show in this paper that *Eoxenopoides reuningi* is a pipid closely related to *Xenopus*, perhaps closest to the relatively generalized species *X. muelleri*, but specialized in a number of features, notably the short vertebral column (six presacrals) and in lack of teeth on the maxilla and premaxilla.

GEOLOGICAL AGE AND PROVENANCE OF *EOXENOPOIDES REUNINGI*

The specimens of *Eoxenopoides reuningi* were taken from sediments filling one of a series of volcanic pipes on a farm near Banke (or Banker) in the Gamoep area near Platbakkies, Namaqualand, Republic of South Africa (30°22′S 18°26′E, 3018 AD Platbakkies sheet, first edition, Geological Map of South Africa, 1: 50 000). The pipe in question is probably one of the group immediately south of the Kimberlite group marked on the 1970 edition of the Geological Map of the Republic of South Africa, Kingdoms of Lesotho and Swaziland, 1 : 1 000 000.

The specimens occur both in black carbonaceous and greenish clays deposited in a temporary lake that developed in the eroded basin or crater of a volcanic pipe about 280–325 metres in diameter, following cessation of the volcanism. The volcanic pipe cuts crystalline metamorphic rocks of Precambrian age. At least 33 metres of clays were deposited in this particular trap, and fossil frogs occur throughout this thickness at the type locality although most of the material came from dumps around the edge of the pipe and was consequently from the upper part of the section. Above the black and green clays a white clayey deposit occurs, and in a near-by excavation a white clayey sandstone contains fragments of fragile green mudstone like that in which the frogs occur. The sandstones are derived from weathering of local basement rocks (gneisses) and although they cannot be traced laterally, Haughton (1931) noted their similarity to the Kangnas sands near by, below which a specimen of the iguanodont dinosaur *Kangnasaurus coetzeei* was found; he therefore suggested that the clays containing the frogs might be 'contemporaneous with or slightly later' than the dinosaur-bearing sediment and thus of late Cretaceous or early Cenozoic age. The dinosaur remains are not reworked, but Anthony Tankard (1976 *in litt.*) has confirmed that there is no direct evidence for this correlation; it should therefore be discounted in an age determination for *Eoxenopoides reuningi.*

Recent radiometric dates on an olivine melilitite pipe on the farm Dikdoorn, south of Garies, gave an age of 38,5 m.y. (Kröner 1973) or about late Eocene age. Andrew Moore (1976 *in litt.*) notes that as yet there has been no date on the similar melilitite cluster of pipes in the Gamoep area although they are assumed to be of the same age. The Banke pipe, capped by sediments that yielded the flora and fossil frogs, however, seems to have a distinctly different chemical imprint from the olivine melilitite suite and thus may be of different age from that given above. Moore further notes that a late Cretaceous to early Cenozoic age for the pipe at Banke, as suggested by Haughton, would indicate that the pipe is of similar age to a phase of volcanic activity that produced pipes on the southern margin of the continent dated at 58 m.y. (Palaeocene) (Dingle & Gentle 1972). Unfortunately, both Haughton's and Moore's suggestions are circumstantial, and lacking a radiometric date on the Banke pipe its age and that of its overlying sediments must on geological grounds still be regarded as speculative.

Along with the publication of Haughton's paper, three papers on associated plant material appeared (Rennie 1931; Adamson 1931; Kirchheimer 1934); none of them gave any specific age determination for the sediments in which both frogs and plants were found. More recent knowledge indicates, however, that a somewhat more specific determination is possible. The pollen described by Kirchheimer has been mentioned by Cranwell (1961), who noted that similar pollen types have been found in 'rather younger' (Oligocene) deposits of Kerguelen Archipelago (Cookson 1947). The leaf flora offers more specific limits. D. I. Axelrod (1976 *in litt.*) believes that the size relationships of the leaves and their sclerophyllous nature indicate a relatively dry climate, with rain limited to the warm season. Based on comparisons with other known fossil floras, the leaf flora is unlikely to be older than later Eocene and not much younger than Miocene, according to Axelrod's determinations.

If the rather circumstantial evidence from the floral remains is accepted, the age range for *Eoxenopoides reuningi* would be late Eocene through Oligocene, a determination that is in accord with the radiometric dates of 38,5 m.y. on the Garies pipes, as well as with the rather tenuous correlation with the Kerguelen sequence suggested by Cranwell (1961). As these suggestions are all compatible this range is taken as the most acceptable one at present, one based on both geological and fossil data. If Moore's suggestion that difference in chemical imprint between the Banke and olivine melilitite pipes indicates an earlier age can be confirmed by a radiometric date, this estimate of age must be revised downward; a Palaeogene age, however, seems to be compatible with both suggestions.

MATERIALS

The collection has not been increased beyond the materials available to Haughton (1931), and includes the original series collected by E. Reuning as well as the later systematic collection of L. D. Boonstra that was correlated more or less with depth of excavation. Haughton gave his series the informal numbers 1–44; of these only 3–7, 9–14, 16–18, 20–21, 23, 35, 40 and 43 still retain these numbers and could be checked against Haughton's description. Subsequently the best specimens have been given South African Museum (SAM) numbers 9938–9965, K4596–K4628, and K4633–K4636; each number may include the remains of more than one individual. There are in addition perhaps 50 fragmentary specimens that are not well enough preserved to be informative. In the discussion below, the SAM numbers are used; Haughton's informal numbers are appended in cases in which reference to his description is made.

Some of Haughton's specimens have been covered with a layer of shellac that has hardened and darkened over the years to an extent that confirmation of his findings on individual specimens is now often difficult or impossible. There is, fortunately, abundant material not so treated and in which preservation is excellent; thus few significant aspects of the osteology of *Eoxenopoides* remain in question.

REDESCRIPTION OF MATERIALS

Holotype

SAM–9938 in the South African Museum, Cape Town. Complete adult frog, Banke, near Platbakkies, Namaqualand, Republic of South Africa. Collected by E. Reuning.

The general proportions of *Eoxenopoides* are shown in Figure 1; it is a relatively compact-bodied frog with relatively large hind feet. Skull proportions of the most common size group appear in the restorations of Figure 2; age changes in skull proportions are shown in Figure 3.

Premaxilla

Haughton's description of these bones in SAM–9948 (H6) was actually based on the nasals (see below). The premaxillae are poorly preserved on all specimens but are best seen on SAM–9941. Teeth are absent (e.g. SAM–K4635). The bones are paired, their median suture overlapped ventrally by the anterior end of the parasphenoid. Their lateral expansions complete the arcade of the upper jaw by fitting into excavations on the anteromedial sides of the maxillae. The prominent alary (nasal) processes are separated on the midline by the anterior ends of the nasals, and appear to be somewhat expanded dorsally (Fig. 2).

Maxilla

The maxilla is well preserved on many specimens, e.g. SAM–9940, 9941 and K4633 (Fig. 2). It is a very long bone, extending far anteriorly in front of the

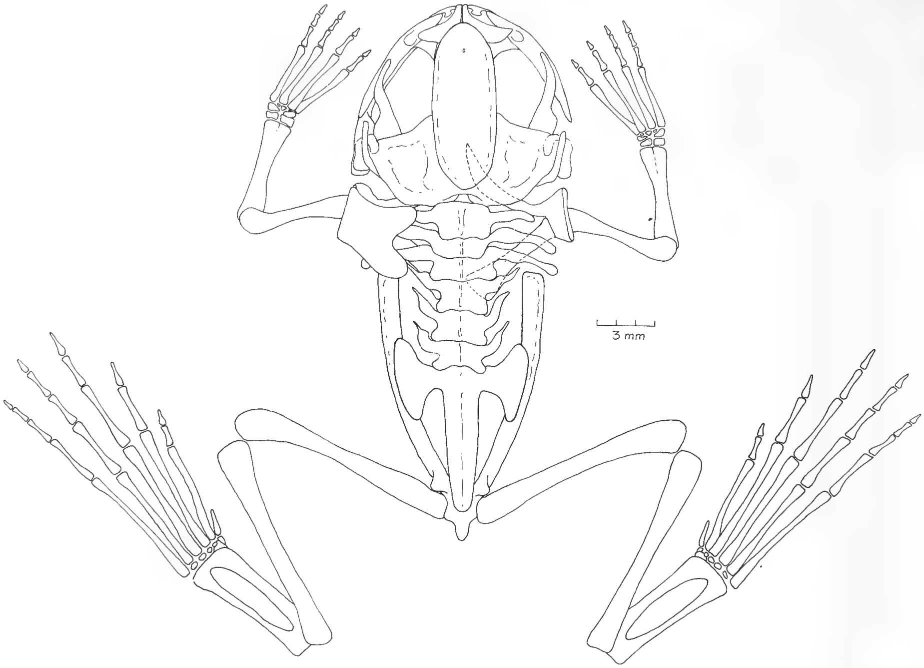


Fig. 1. *Eoxenopoides reuningi.* Restoration of skeleton in dorsal view. Cleithrum and lower jaw removed on right. Dashed line indicates extension of elements of shoulder girdle ventral to skull and vertebral column.

premaxillae to the alary processes of the latter, and posteriorly reaching or exceeding the posterior border of the palatal vacuity. It is flattened dorsally and expands anteriorly into a spoon-shaped process, the cavity of which opens posteriorly into a large circular foramen extending into the body of the bone (Fig. 4A–B). Its ventral edge is toothless but forms a sharp ridge (pars dentalis) that marks the oral margin. Its posterior end is pointed.

Lachrymal

No lachrymal is present. The element so identified by Haughton is a part of the ossified planum antorbitale (see below, sphenethmoid).

Nasal

The nasals are best shown on SAM–K4596a, K4605a, K4615 and K4616. They are semicircular paired bones lying on the borders of the nares and partly overlapping the frontoparietal (Fig. 2A). Laterally they are flattened and teardrop-shaped; on the midline, their closely approximated tips curve ventrally, forming two narrow, strap-shaped processes that separate the alary processes of the premaxillae.

Haughton identified what is actually the cracked anterior end of the frontoparietal in SAM–9939 (H21) as fused nasals, and identified the actual nasals of SAM–9948 as premaxillae. The 'lateral spurs' of Haughton's presumed nasals, however, are in fact those bones, representing their maxillary (lateral) processes. The median foramen on the 'nasals' figured by Haughton (1931, fig. 1) is the parietal foramen, in its normal position on the anterior end of the frontoparietal.

Frontoparietal

This large bone is visible on most specimens, but only a few examples are not cracked or distorted; best preservation is seen on SAM–9965, K4596, K4597, K4599, K4601, K4602 and K4608c. It is a single bone rather than being paired as indicated by Haughton, broadly ovoid, bluntly rounded anteriorly and somewhat more pointed posteriorly (Figs 2A, 3). Its dorsal surface is relatively smooth and flat, with a faint thickening of the lateral edges, but in younger specimens the frontoparietal surface may be faintly convex. Haughton cited the frontoparietal as 'depressed longitudinally in the middle', but this is the result of crushing. The parietal foramen is prominent and placed far forward, about 13–15 per cent of the total length from the anterior end.

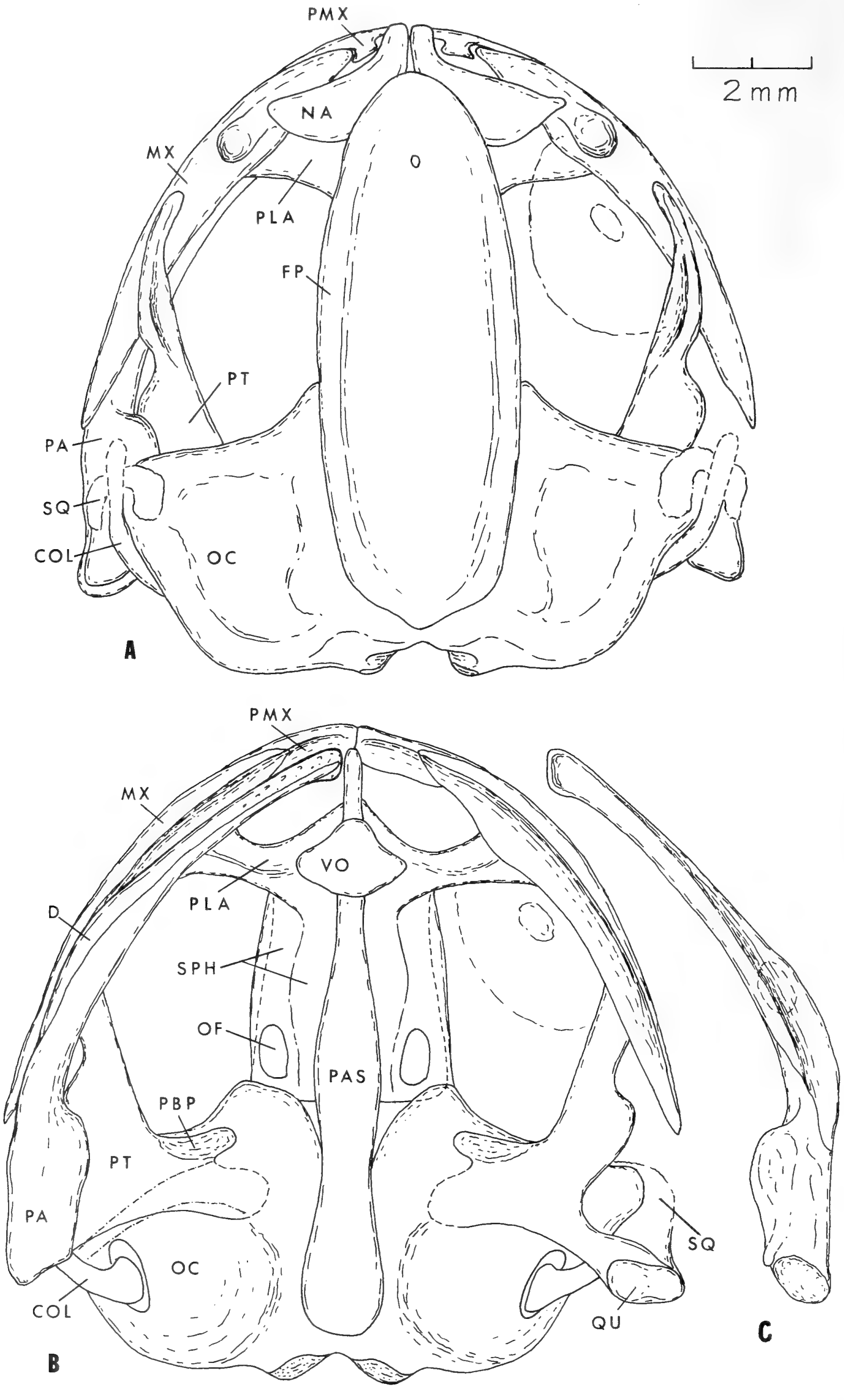
SAM–9939, on which Haughton's figure 1 was based, has been severely damaged by dried, cracked and exfoliated shellac and is difficult to interpret. It is clear, however, that the posterior area suggested by him as having contained a cartilaginous supraoccipital is actually a crack and that the bone he suggested as being a scapula or opisthotic is actually a fragment of cleithrum.

Otoccipital

The shape of the paired otoccipitals is shown on many specimens, in particular SAM–9941, 9944, 9946b, 9965, K4609, K4610b, K4620f and K4626b. They are large and concave dorsally, with outlines of the semicircular canals prominent (Fig. 2). Ventrally the otoccipitals do not meet on the midline anteriorly (SAM–9941), and each otic region is inflated into a hemispherical chamber anterior to which there is a prominent channel for the eustachian tube. Lateroventrally in SAM–K4610b the fenestra ovalis is visible, partially occluded on the right by the columella. Posteriorly the otoccipitals meet on the midline dorsally (SAM–9946, K4603d) and fuse ventrally, forming the occipital condyles (SAM–K4610b). Small protuberances for cervical muscle attachment occur on the posteromedial ends of the otic capsules (SAM–K4603d, K4609a). No foramina are visible.

Columella

The plectrum of the columella is shown in few specimens, but in SAM–K4610b it is visible ventrally, in natural position in the fenestra ovalis (see Fig. 2). A boomerang-shaped bone, it extends anterolaterally from the fenestra ovalis, then abruptly bends anteriorly and extends forward perhaps as far as the posterior tip of the maxilla (SAM–9965, although some forward displacement of the columella has taken place here). No trace of operculum is present.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Sphenethmoid

The sphenethmoid is well developed (Fig. 2B); in all examples it is a single ossification that extends posteriorly almost to the posterior borders of the palatal vacuities (SAM–9941, K4600d, K4635). Just anterior to this point, large optic foramina are visible (SAM–9941, K4609b, K4635). Crushing has usually obscured the contours of the sphenethmoid, but in SAM–9941 and 9940 particularly it is clear that its apparent wideness (observable on many specimens) is not the result of crushing. In these two specimens the lateral sides are seen to converge ventrally from their contact with the frontoparietals, and form a broad wedge-shaped bone whose laterally-keeled, flattened ventral surface is capped by the long, narrow parasphenoid. Anteriorly, as the sphenethmoid expands laterally into the planum antorbitale, there is a constricted region (SAM–9941, K4597c, K4609b). Anterolaterally, the arms of the planum antorbitale extend to the maxilla (SAM–9955, K4597c). The smooth ventral and posterior surfaces of the planum antorbitale suggest that this region is ossified, with the formation of a lamellar surface layer, rather than being calcified. On SAM–9940 a cross-section reveals the presence anteriorly of paired internal channels for the olfactory tracts, lined with smooth lamellar bone.

Palatine

No trace of this bone can be seen, although it may be present and fused to the planum antorbitale.

Vomer

In SAM–K4614c, 9940 and K4609b, cross-sections show that the rod-like cultriform process of the parasphenoid, anterior to the sphenethmoid constriction noted above, overlies a roughly polygonal layer of bone that can only be fused vomers, distinct but fused to sphenethmoid and parasphenoid (Fig. 5A). In another specimen (SAM–K4635) no bone underlies the ventral surface of the parasphenoid in this region, indicating that the vomer may sometimes remain unfused (in this case lost).

Parasphenoid

Shape and form of the entire parasphenoid is shown well only in relatively young metamorphosed (SAM–K4603b) or in late tadpole (SAM–K4612a, K4613a) stages (Fig. 6A). It is a long, narrow bone, expanded very slightly in its midportion in tadpole stages but more so in adults (SAM–K4597a), an expan-

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Fig. 2. *Eoxenopoides reuningi.* A. Dorsal view of restored skull. B. Ventral view. Based primarily on SAM–9940, 9941, K4596a, K4606a. Lower jaw removed on right side of dorsal view, left side of ventral view. Squamosal outlines and anterior extent of columella somewhat conjectural (see text). Dotted-dashed line indicates approximate position of eustachian tube. Note impression of eyeball and iris. C. Lower jaw in dorsal view. Composite of K4599a, dentary, and K4606a, postdentary complex; position of large internal dentary foramen shown in dotted line (see Fig. 4A for comparable foramen in maxilla).

sion that does not exceed one-half the maximum width of the frontoparietal in any individual (Fig. 2B). Its anterior end is narrow and pointed, overlapping the premaxillae; posteriorly the bone narrows between the otoccipitals and terminates near the posterior border of the skull in a spatulate tip (SAM–K4602b).

Pterygoid

This is a well-developed bone (SAM–9940, 9941, 9955) extending anteriorly as a wide curved blade; as it reaches the maxilla it narrows, forming a channelled tip (SAM–9940) that overlies the maxilla, curving along with the latter until it terminates at or beyond the level of the posterior border of the planum antorbitale (Fig. 2). Posteriorly a thin process extends towards the quadrate region, curving ventrally into a sharp ridge (SAM–9955, H14). Posteromedially, a flattened process extends from this ridge to floor the eustachian tube region; it terminates near the midline in a point (SAM–9940), underlying (or perhaps abutting) the pseudobasal process.

Quadrate

In most cases the quadrate is obscured by the lower jaw, but it appears to have been well ossified (SAM–9940), and not unusual in general aspect (Fig. 2).

Squamosal

Indistinct fragments are all that can be seen of the squamosal; crushing and displacement of what must have been a lightly ossified bone has left little to interpret. The bone was small and seems to have encircled the columella; no processes can be seen, but on SAM–9965, K4596a and K4601 it seems to have formed a conch within which the columella lay (see Fig. 2).

Mandible

This is best shown in SAM–9940, 9941, K4597c, K4599a, K4606a and K4614c (see Fig. 2). The mandible is usually rather poorly preserved and crushed in articulated specimens and is often difficult to distinguish from surrounding bones. Examples of this condition are seen in SAM–9940 and 9941. A perfectly preserved isolated dentary has been extracted from specimen SAM–K4599a. Posteriorly the dentary is expanded and keeled laterally (Fig. 2); anteriorly it is widened at the symphysis, rather flattened both dorsally and ventrally, and perforated with numerous small foramina. No symphysials (mentomeckelians) were observed on any specimen and the close approach to each other of the dentaries at the symphysis region indicates that they were not present. The prearticular is well shown in a number of specimens, in particular a perfectly preserved isolated specimen SAM–K4606a (Fig. 2c). It is long and sharply pointed anteriorly and complex posteriorly, where it includes the fused articular. Its posterior end (SAM–9940, K4597a, K4606a) is flattened and expanded, the adductor muscle attachment surface prominently developed with a squared-off anteromedial

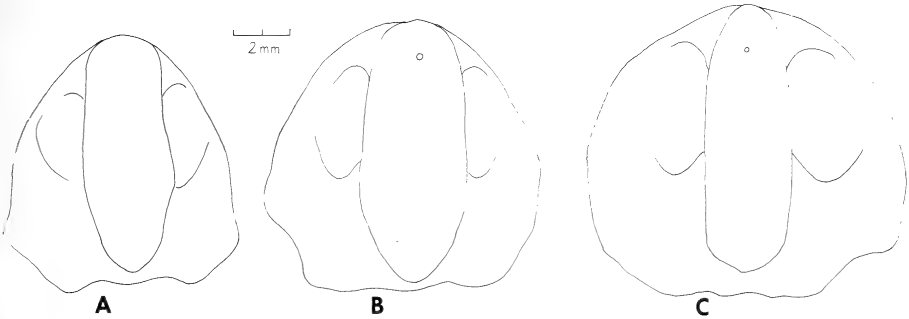

Fig. 3. *Eoxenopoides reuningi*. Relative growth of skull. A. SAM–K4608c, skull length 8,8 mm. B. SAM–9965, skull length 9,4 mm. C. K4596a, skull length 10,9 mm.

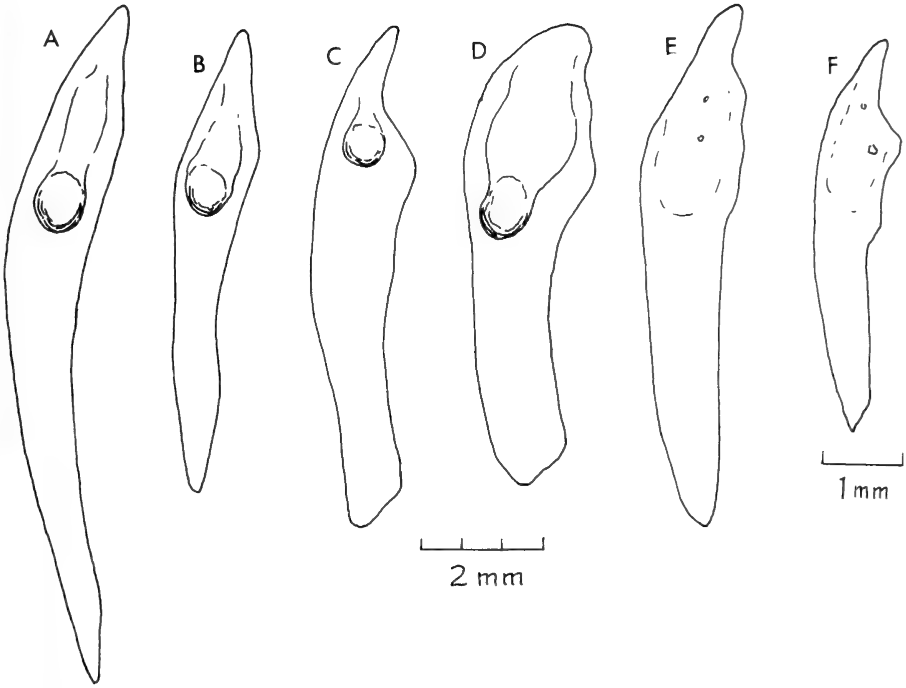

Fig. 4. Left maxillae of various pipids in dorsal view. A. *Eoxenopoides reuningi*, SAM–9940. B. The same, SAM–K4596c. C. *Xenopus muelleri*. D. *Xenopus tropicalis*. E. *Xenopus laevis*. F. *Xenopus vestitus* (the same configuration is seen in *X. gilli*, *X. clivii* and *X. fraseri*).

border. Anteriorly the bone extends almost to the symphysis as shown in articulated material.

Vertebral column

The method of vertebral articulation in articulated specimens cannot be seen, but SAM–4623b, an isolated vertebra, shows the presence of an anterior condyle, indicating an opisthocoelous column. SAM–K4618a, the cross-section of an isolated vertebra, indicates that the vertebrae were probably epichordal, as no significant expansion of the centrum region occurs.

There are only six presacral vertebrae in all specimens in which the full column is present (Fig. 1). Haughton believed that either six or seven might be present, but careful examination of all specimens available failed to disclose more than six. The first vertebra is elongated and bears a long transverse process, indicating that the true first vertebra (cervical vertebra or 'atlas') is fused with the second presacral vertebra. This is confirmed in one of the tadpole specimens (SAM–K4613a), which has a suture separating the two vertebrae (Fig. 6B–C). In subsequent discussion, the fused cervical and second presacral will be referred to as the first presacral to avoid confusion. The transverse processes of the first three presacral vertebrae are elongated; the tips of most examples are broken but the second and third are complete and subequal in length in SAM–9940 and K4626b, the third complete in K4609a. In K4626b expansions of the transverse processes near the centrum perhaps indicate the points of rib fusion but separate ribs do not occur. Because of closeness to the skull, the shape of the first transverse process is generally not clear, but on SAM–9946, K4609a, and K4626b it appears to be shorter than the second and third, and curved anteriorly, fitting closely to the skull. Transverse processes of vertebrae 4–6 are relatively shorter, anteriorly directed, somewhat expanded at the base and sharply pointed distally (SAM–K4609a).

The centra and neural arches are blocky, the zygopophyses simple and not strongly projecting. The ventral surfaces of the centra appear somewhat bulbous on each side of a shallow midline depression. Dorsally, there is no trace of a neural spine or crest on the neural arch surface in most specimens (e.g. SAM–9939) but occasionally (SAM–K4634) the posteromedial border of the neural arch forms a minute projection. The posterolateral borders of the arch are slightly concave whether or not this projection is present.

The sacrum and urostyle are fused and there is no trace of a postsacral vertebra except on SAM–K4636 (Fig. 7C). The sacral diapophyses are widely expanded on all specimens, at their tips approximating the length of the last three presacrals.

Haughton discussed a number of 'morphological stages' that represent variation in the vertebral and sacral region. His stage 'A' is misinterpreted; the single specimen on which it is based (SAM–9945, H17) has a series of cracks in the sacral diapophysis rather than a series of diapophyses, and as noted above, there are always six presacrals rather than 'not greater than seven'. Haughton's

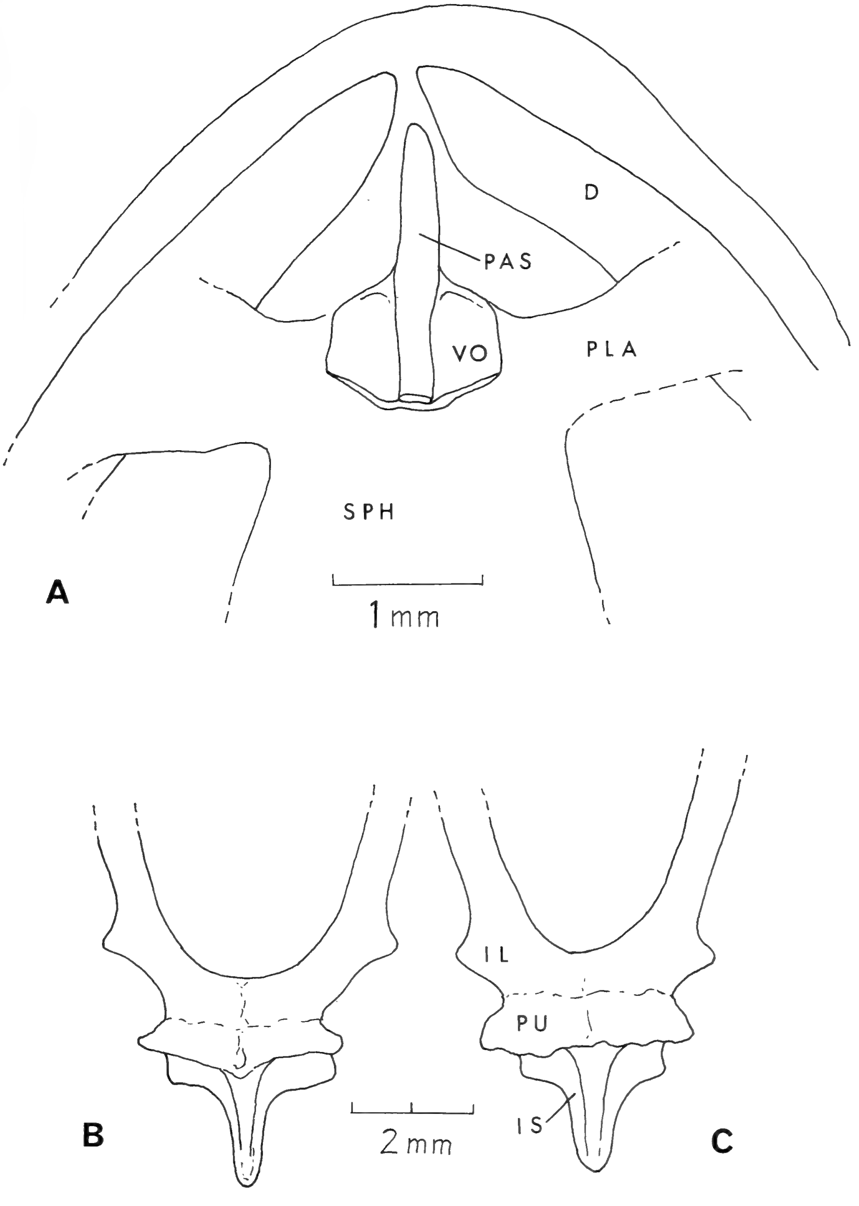

Fig. 5. A. *Eoxenopoides reuningi*, SAM–K4614c, dorsal view of ventral snout region, split in a plane immediately dorsal to the parasphenoid and planum antorbitale. Note vomer ankylosed to ventral surface of parasphenoid but remaining distinct from it. B. Ventral view of posterior region of pelvis of *Xenopus muelleri*. C. The same view of *Eoxenopoides reuningi*, SAM–9945.

stage 'B' is the most common (85 % of specimens examined in which this region could be interpreted clearly; n = 27); it is the unmodified condition, with normal development of sacroiliac articulation and transverse processes (Fig. 1). As Haughton indicated, there are in this stage only six presacral vertebrae. Examples of this configuration are many, the best ones including SAM–9938, 9942, 9956, 9964, K4596a, K4597d, K4603, K4609a, K4611, K4620, K4622, K4626 and K4627. Haughton's stage 'C' could not be confirmed on the three specimens for which he cited it: SAM–9948 (H6) and 9960 (H7); H22 could not be found and lacks a SAM number. In SAM–9948 the left transverse process of the last presacral is somewhat longer than usual, but is not sacralized. In K4596c, however, a specimen not mentioned by Haughton, the left transverse process is expanded and sacralized, that on the right somewhat enlarged. This is the closest approximation now available for stage 'C' (Fig. 7B). Stage 'D' of Haughton is valid, based only on the specimen SAM–9946 (H23; Fig. 7A). There is a double sacrum, the sixth (last) presacral having been completely sacralized yet remaining suturally separate from the true sacrum. This is similar to specimen F24 of the early Cretaceous pipid *Thoraciliacus* in which it appears in 2 of 247 specimens (0,8 %; Nevo 1968). Stage 'E' of Haughton was cited as present in SAM–9942 (H11) and was presumed to represent a stage having only two vertebrae with short, anteriorly directed transverse processes rather than three, and with a postsacral vertebra showing transverse processes. This specimen is actually a stage 'B' with six presacrals and no postsacral vertebra visible. The closest approximation to this stage that could be found was in SAM–K4636, in which a fused postsacral vertebra with large transverse processes is visible, the right one fused to the sacrum; in this specimen the normal six presacrals are present so that this does not represent a stage 'D' (Fig. 7C). Haughton's 'anomalous' stage, with asymmetry of sacral transverse processes, is well shown in the single specimen on which he described it (SAM–9965, H40); only the right transverse process of the last presacral and the left transverse process of the sacrum are sacralized. This is a common anomaly in frogs, both recent and fossil; Nevo (1968) has described it in the Cretaceous pipid *Thoraciliacus* (specimen F128), finding it in 3 of 247 specimens (0,8 %), and Ritland (1955) observed it in living *Ascaphus*.

Shoulder girdle

The coracoid and clavicles are widely divergent and the clavicles do not meet in a broad suture; the girdle was therefore presumably arciferal, although without the cartilaginous epicoracoid horns this cannot be confirmed. The coracoids are very slightly expanded at their medial ends (Figs 1, 8). A prominent groove is present on the dorsal surface of the clavicles. The junction of scapula and clavicle is difficult to interpret owing to poor preservation in all specimens, but is relatively clear in SAM–9940 and 9948 (H6). The scapula is relatively long and somewhat expanded anteriorly; the presence of a cleft is not determinable. On SAM–9940 it appears that there was a suture between scapula and clavicle, but this may be a crack, for several other cracks are present in the body of the clavicle

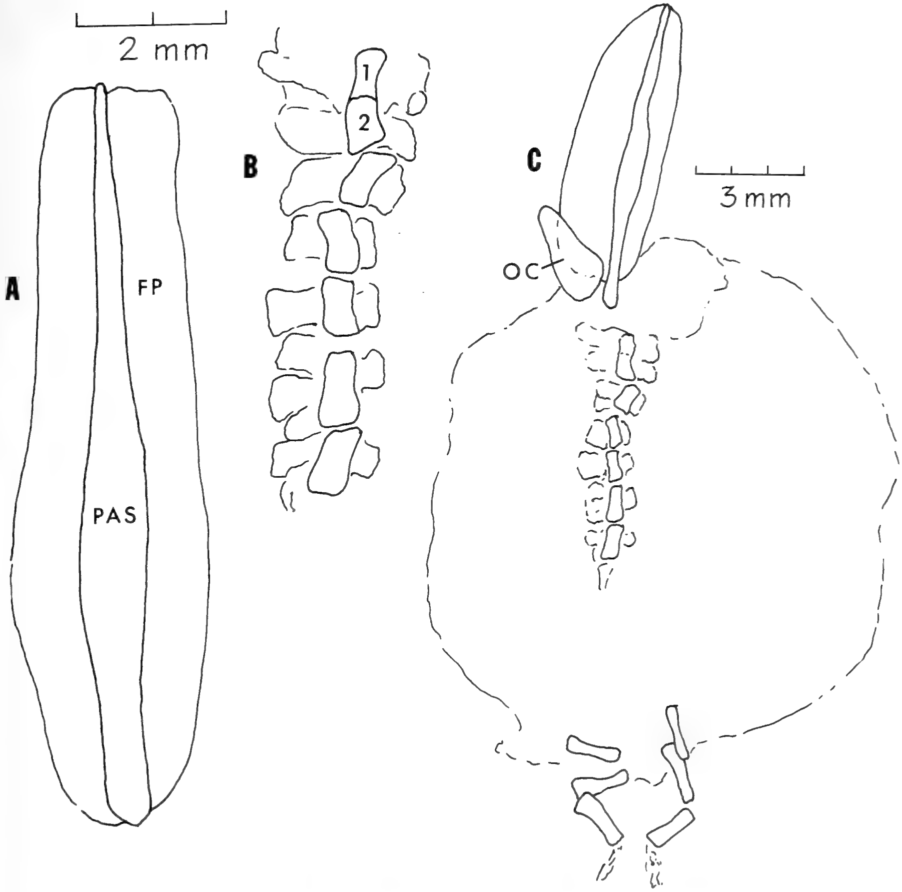

Fig. 6. *Eoxenopoides reuningi*, tadpoles. A. SAM–K4612a, ventral view of frontoparietal and parasphenoid. B. SAM–K4613a, vertebral column showing partial fusion of first two presacral vertebrae. C. Ventral view of same specimen, showing partially ossified otic capsule, outline of body cavity, and hind limbs.

(see below). The cleithrum is widely forked and shown well on SAM–K4596a, K4615c and K4626b. The questionable cleithrum noted by Haughton is correctly identified, but is seen folded over on the scapula rather than its normal more dorsal position; it is thus not applied to the anterior margin of the scapula as Haughton supposed.

Humerus

In crushed form, the humerus is visible on many specimens (Fig. 1). Fortunately, an uncrushed isolated left humerus was prepared from SAM–K4610a and shows that the humeral head has a prominent trochlea for articula-

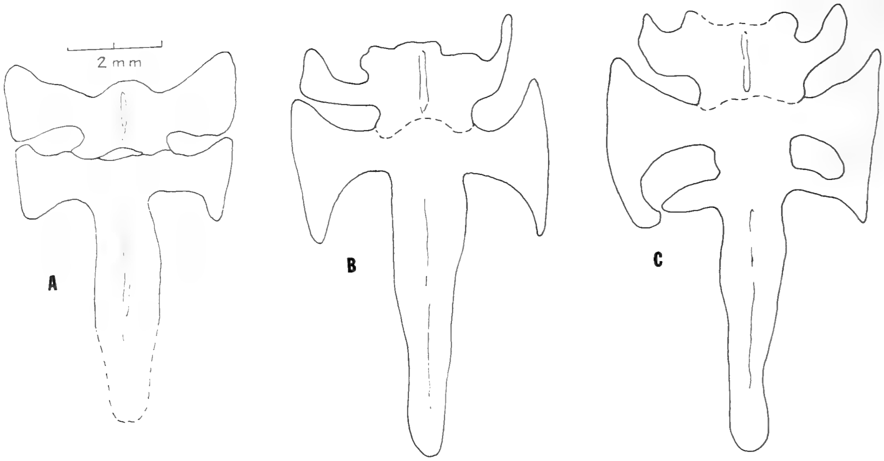

Fig. 7. *Eoxenopoides reuningi*, variation in sacro-urostyle (see text). A. SAM–9946. B. SAM–K4596c. C. SAM–K4636.

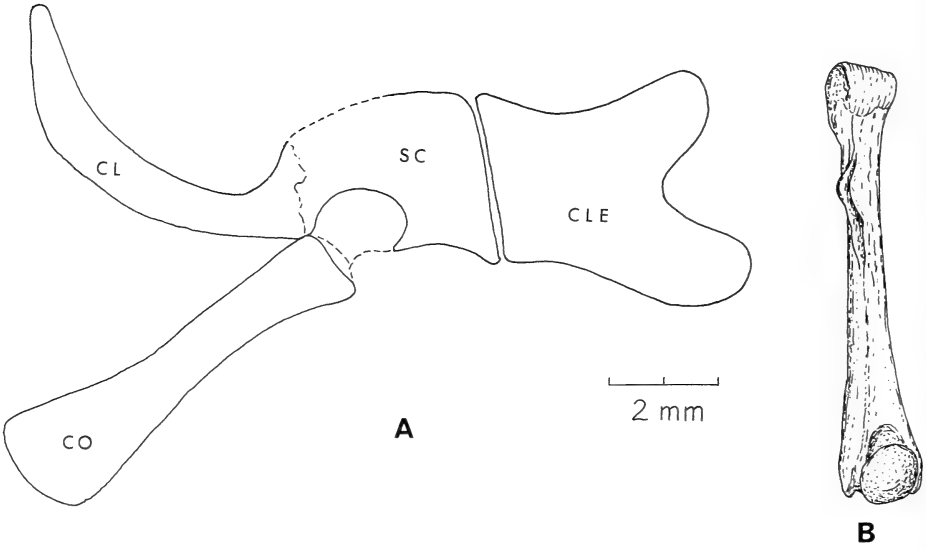

Fig. 8. *Eoxenopoides reuningi*. A. Restoration of shoulder girdle, rotated so that all bones appear in the same plane. Based primarily on SAM–9940 and 9948, cleithrum from SAM–K4615c. B. K4610a, left humerus in ventral view.

tion with the scapula, from which a prominent crest extends distally to meet the deltoid crest on the shaft. A deep channel occurs on the medial surface of the deltoid crest, set off by another crest lateral to it. Distally the humeral ball is small, as are the epicondyles; the *fossa cubitus ventralis* is prominently marked (Fig. 8B).

Radioulna

The radioulna is of usual anuran form (Fig. 1), fused, slightly expanded distally, and with a prominent fossa proximally for the ball of the humerus.

Carpus

SAM–K4611 (H11), in which Haughton described the carpus, no longer has that region preserved. Fortunately, K4599b, K4609b (Fig. 9A), K4615c and K4627 show reasonably well-preserved carpal arrangements in both ventral and dorsal views. Two main elements in the proximal row of the carpals represent radiale and a large ulnare; the latter has a prominent ventromedial process shown well on two specimens that probably represents the fused intermedium (Fig. 9B). Distally there are again two main elements: a lateral one probably representing the fourth distal carpal, clearly shown on K4615c to include another element medially, probably the third centrale, and a medial, subtriangular bone that represents at least the second centrale. Distal carpals 1–3 are shown on K4627b, as well as a small medial bone that represents the prepollex (or first centrale).

Metacarpals and phalanges

There are four metacarpals, well shown on SAM–K4599b, K4603a and K4609b. Distally these three specimens show that the phalanges are relatively short and that the phalangeal count is 2–2–3–3. Digit length increases progressively from digits 2–5, but the fingers are not much different in length (Fig. 10A).

Pelvic girdle

The proportions of the pelvic girdle as a whole are shown on numerous specimens, among them SAM–9938, 9945, K4597f and K4609a. The ilium is well seen in dorsal view on K4609a. No specimen permits a lateral view of the acetabular region, but the general shape of the ischium and pubis area is shown in K4609a and 9945 (Fig. 5C). The ilium is elongate and there is an iliac symphysis proximally on the midline. The iliac shaft on most specimens extends far forward, nearly or actually touching the transverse processes of the third vertebra (SAM–9965) but in others terminates near the end of the sacrum (SAM–K4596c). The iliac shaft is robust but only a small iliac crest is present. The dorsal protuberance is well developed but low and rounded, not protruding far from the shaft. The ischium is usually obscured by the urostyle, but in SAM–K4609a it is well ossified and robust (Fig. 5C). The pubis is well ossified as shown in SAM–9945,

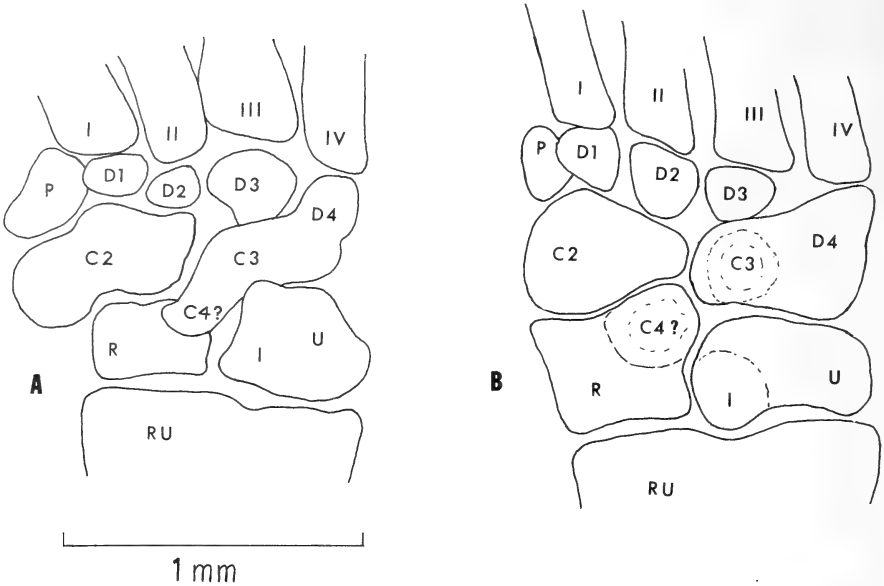

Fig. 9. A. *Xenopus muelleri*, right carpus in dorsal view. B. *Eoxenopoides reuningi*, restoration of carpus, based primarily on SAM–K4615c and K4627b. Note position of ventral impressions of intermedium and central elements three and four, indicated in dotted line.

and forms a prominent transverse crest on the ventral surface of the pelvic girdle; as in most recent pipids it is smoothly ossified rather than calcified (Fig. 5C).

Femur

The general shape of the femur is visible on many specimens. It is relatively slender but well ossified. No details that indicate notable features are visible (Fig. 1).

Tibiofibula

The general shape of the bone is visible on many specimens. It is not notable in any way (Fig. 1).

Tarsus

Tibiale and fibulare are intimately fused. This is visible externally on many specimens, and a split longitudinal section (SAM–K4598a) shows that this fusion extends to the interior of the bones as well as to the epiphysial caps; the fused bones have a common cavity.

A central element associated with the fibulare, one for the prehallux, and a distal tarsal for the first metatarsal are visible on SAM–9945; centralia associated with fibulare, prehallux, and metatarsals 1–3 on 9959; on K4609a distal tarsals 1–4 are visible, as well as the centralia for the prehallux and fibulare (Fig. 10C).

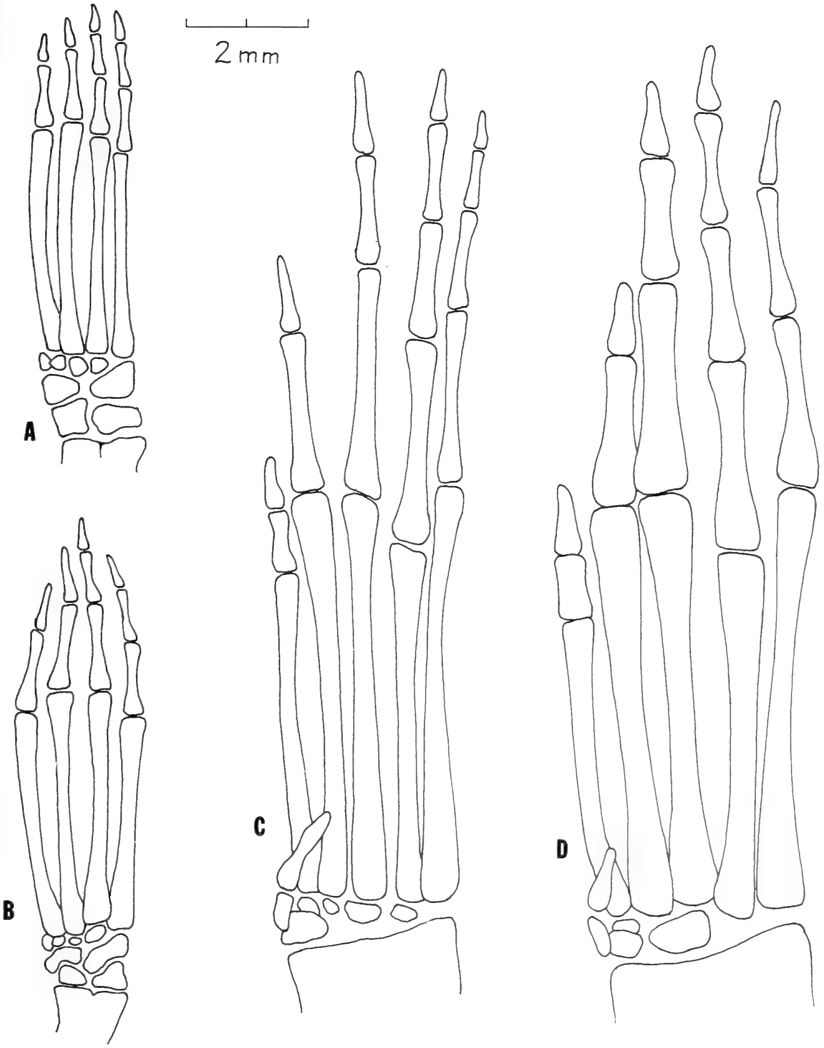

Fig. 10. A–C. Comparison of right dorsal surfaces of hand and left ventral surfaces of foot of *Eoxenopoides reuningi*. B–D. The same of *Xenopus muelleri*. A based on SAM–K4603a, K4615c and K4627b, C based on K4609a; both specimens are from animals of equal size.

Metatarsals and phalanges

These bones are well shown on many specimens but are completely preserved on SAM–K4609a (Fig. 10C) and K4624b. They are elongated but not unusual in any way.

The phalanges are generally not well preserved but are complete on SAM–K4609a (Fig. 10C), K4624b and, except for the first digit, on K4627a and

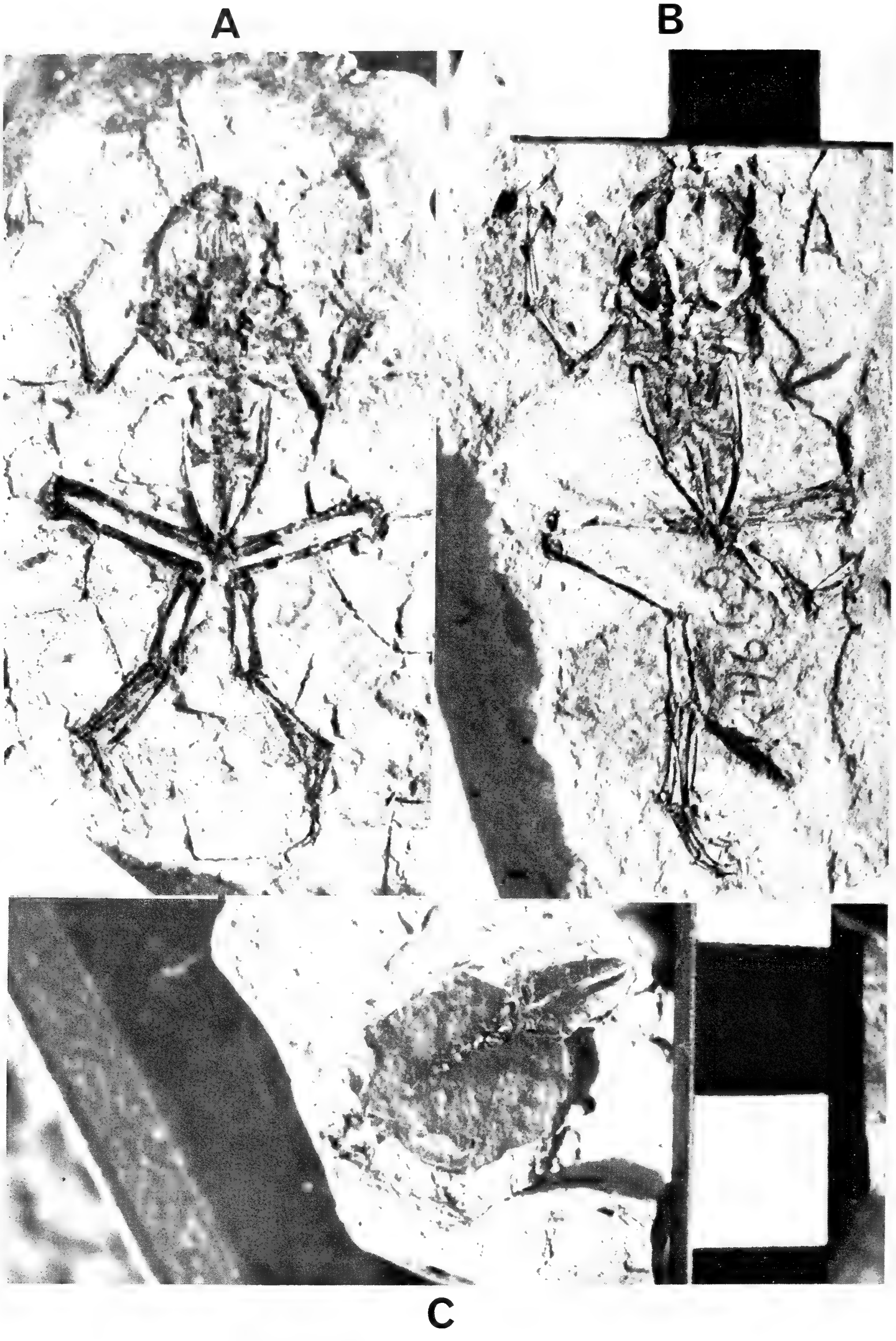

Fig. 11. *Eoxenopoides reuningi*. A. SAM–9938, holotype. B. SAM–K4609a, natural cast of dorsal surface of skeleton (except for a few regions, including the hind foot, where bone is still present). C. SAM–K4613a, tadpole, note outline of body cavity left by melanophore concentration. Scale in centimetres.

K4627b. They are relatively short. The prehallux is represented only by a single phalanx, seen well in SAM–9945 and 9959 as well as on K4609a. SAM–K4609a and K4627a are well preserved and show that the phalangeal formula of digits 1–5 is 2–2–3–4–4; K4627b demonstrates with equal clarity that 2–2–3–4–3 may occur as well. In the latter case the terminal phalanx is reduced and pointed, indicating that this is of natural rather than of taphonomic origin, although traumatic loss during the life of the animal cannot be ruled out.

COMPARISONS

Eoxenopoides reuningi possesses the suite of pipid character states given by Estes (1975*a* and 1975*b*) and no question exists as to its family allocation, as will be demonstrated below. Comments on the structure of *E. reuningi* follow the sequence of bones given in the description.

The maxillae are remarkable in that their anterodorsal surface is almost identical with that in *Xenopus muelleri* and *X. tropicalis* in having an oral depression with a large posterior foramen that opens into the body of the bone. No other species of *Xenopus* nor species of other pipid genera show this configuration. The absence of teeth on the maxilla is unlike all pipids save some of the South American species; this is not in any case a character state of more than specific importance.

The nasals are paired, but otherwise resemble closely those of living *Xenopus*, especially in having long, slender processes anteromedially that overlie the nasal capsule and separate the alary processes of the premaxillae. The nasals may occasionally remain paired in adult living *Xenopus* although usually they are fused.

The frontoparietal is unlike that of any known pipid in detail, but resembles that of the fossil *Xenopus romeri* in having an extensive dorsal skull table, essentially parallel sides, and an anteriorly placed parietal foramen (Estes 1975*b*). It differs from that of all species of *Xenopus*, however, and resembles *Hymenochirus boettgeri* and *Pipa* spp. in lacking muscle attachment on the dorsal surface of the frontoparietal. Lambdoid crests are thus not developed except on the lateral edge of the bone, and weak supraorbital ridges are present.

The otoccipital resembles that of *Xenopus* in detail, especially ventrally, in which the expansion of the inner ear region and the configuration of the eustachian tube channel closely resemble conditions in Recent *X. muelleri* and the fossil species *X. romeri* and *X. pascuali*. The pars media plectri of the columella is well ossified, and bent into a boomerang shape, with otic and tympanic processes as in *Xenopus* spp.

The sphenethmoid is widened dorsally, reflecting the width of the dorsal table of the frontoparietal, which its laterodorsally diverging sides meet. Two distinct internal channels for the olfactory tracts occur as in pipids in general; the lack of flattening of these channels and their close approximation is as in *Xenopus* spp. rather than in living South American species.

The apparent rhomboid, toothless shape of the vomer and its tendency either to fuse to the sphenethmoid and parasphenoid or to remain separate is as in *Xenopus romeri* (Estes 1975*a*, figs 1–2). Lynch (1973) and Trueb (1973) have called these bones 'prevomers'. This designation has been shown to be in error by Parrington & Westoll (1940), who demonstrated that the original suggestions of the existence of a separate 'prevomer' in lower vertebrates was a misinterpretation.

The cultriform process of the parasphenoid is narrow anteriorly as in *Xenopus* and the fossil *Cordicephalus*, *Thoraciliacus* (Cretaceous, Israel; Nevo 1968), and *Saltenia* (Cretaceous, Argentina; Báez in preparation), rather than widened as in *Hymenochirus* and the living South American pipids.

Posteriorly, the pterygoids resemble those in pipids generally, with expanded medial processes flooring the common opening of the eustachian tube, but the long, slender anterior process reaching almost to the level of the planum antorbitale is exactly as in *Xenopus* and *Saltenia*, lacking the expansion in that region found in *Pipa*. Such an anterior extension of the pterygoids is also seen in the Cretaceous genera *Thoraciliacus* and *Cordicephalus*, but curvature of the bones appears to have been different in the latter, the anterior ends being laterally concave rather than convex.

The squamosal, while poorly ossified, seems to have enclosed the columella in the usual pipid manner, essentially as a cylinder for the reception of the columella and tympanic membrane. In lacking the strong development of a zygomatic process some similarity to *Hymenochirus* and *Saltenia* occurs.

The dentary differs from that of other pipids in having an expanded symphysis region; in other pipids the dentary tapers to a point anteriorly. The postdentary compound element (articular and prearticular) resembles that of *Xenopus* spp. closely except for being relatively straight at the posterior end rather than having the articular region twisted laterally.

Aside from the reduction in vertebral number, the vertebral column as a whole resembles that of many frogs in having a relatively short first transverse process, posteriorly curved, elongated second and third transverse processes, and short, anteriorly directed and pointed transverse processes of the fourth, fifth, and sixth vertebrae. Among pipids, fusion of cervical and second vertebra is characteristic of all species of *Pipa*, *Hymenochirus* and *Pseudhymenochirus*, *Xenopus tropicalis* and *X. romeri*, and may occur occasionally in large *X. laevis*.

The neural arches are imbricate, their surfaces smooth and their posterior borders slightly concave on each side; the centra are opisthocoelous and probably epichordal. In all these features they resemble pipids as a group.

The fused sacrum and urostyle region resembles that of *Saltenia*, *Thoraciliacus* and *Cordicephalus* in having sacral diapophyses only moderately expanded, to about the length of the last three presacrals rather than equivalent to the length of five or more vertebrae as in other pipid genera. The sacral vertebra is clearly not compound; the necks of the sacral diapophyses are narrow and there is at most one major spinal nerve foramen visible on their posterior surfaces.

Thus in *Eoxenopoides* reduction in vertebral number is partially a result of synostosis (second presacral and cervical) and partially a case of true reduction by deletion of the seventh vertebra through the sacrum (Lynch 1973: 141) and constitutes the second such case described. Tihen (1960) has shown fusion of cervical and second presacral vertebrae and true reduction of the column to seven segments (hence six presacral vertebrae) in the bufonid *Nectophryne*. *Hymenochirus* also has cervical and second presacral fused and only five presacrals in all, as does the bufonid *Oreophrynella*, but in both of these latter two cases the reduction of posterior vertebrae has been effected by synostotic fusion of presacrals with the sacrum, which shows an obvious compound nature, unlike the situation in *Eoxenopoides*.

Broad expansion of sacral diapophyses has been considered primitive in frogs, and Lynch (1973) cites them as 'characterizing the four living archaic families' Ascaphidae, Discoglossidae, Pipidae and Rhinophrynidae. Primitive fossil members of Ascaphidae and Discoglossidae have quite narrow sacral diapophyses, however, and Cretaceous pipids as well as *Eoxenopoides reuningi* have only moderate expansion (see Estes & Reig 1973). There is thus doubt that the expanded condition (at least a widely expanded one) is primitive, as the fossil record does not support this view. The separate sacral ribs of *Triadobatrachus* are somewhat expanded, however, and the picture is therefore not entirely clear. *Triadobatrachus* was very froglike in some respects but it had not yet achieved anuran status, in spite of the statement of Wassersug (1975) to the contrary (see Estes & Reig 1973). It is perhaps best in this case to give greatest weight to true anuran conditions, and the fossil record suggests that an unexpanded or at most a moderately expanded form was the most primitive.

The general configuration of the shoulder girdle does not offer much of comparative interest. Scapula and clavicle are separated by what might be interpreted as a suture in SAM–9940; if it is one the clavicle does not overlap the scapula as much as in other pipids. It is possible, however, that this presumed suture is, in fact, a crack for there is some distortion and several other cracks on the clavicle of this specimen. If scapula and clavicle are fused, the condition is derived, and resemblance is to *Xenopus* (excepting *X. pascuali*); if they are not, the condition is primitive. Because the apparent suture cuts transversely across the bone rather than being on an angle, overlapping the scapula anteriorly as would be expected in a pipid or other primitive frog, the author interprets the scapula and clavicle as having been fused, but broken in an area of relatively weak ossification. This ambiguity is the only one that has affected interpretation of the *Eoxenopoides* fossils but it is not a fundamental one.

The humerus is very like that of pipids in general. The specific details of trochlear head, crests and epicondyle configuration resemble those in *Xenopus* spp. rather than those of the living South American pipids or *Hymenochirus*. Both of the latter groups have either large epicondyles (*Pipa*) or strong development of specialized humeral crests (*Hymenochirus*). The humeral ball is larger and more protuberant than in most living or fossil pipids; only the Miocene

Xenopus from Morocco (Vergnaud-Grazzini 1966) and the Recent *Xenopus tropicalis* approach it in size. This would be a primitive feature, probably, since the result is more like that of other groups of living and fossil frogs.

The radioulna offers no points of special interest.

The carpus is as in *Xenopus laevis* and *X. muelleri*, the only two species for which cleared and stained preparations were available. The chief interest that it offers is the evidence for fusion of carpal elements in pipids, and perhaps for frogs in general. On the ventral view of the large ulnare of SAM–K4615c there is a process probably representing a fused intermedium, as has been demonstrated in living frogs (Trueb 1973). Of more interest is the fourth distal carpal, which shows very well an element that is probably the attached and fused third centrale, as suggested by Trueb (1973) to occur in living forms. The radiale shows a comparable situation; its internal side has a prominent centre of ossification (not a process) that must be the fourth centrale, again as postulated by Trueb (1973). A prepollex or first centrale is visible next to the first distal tarsal. The configuration in *Xenopus* is somewhat different (Fig. 9A); there has been a shortening and torsion of the carpus and the fourth distal carpal is much elongated, firmly abutting and overlapping the radiale, suggesting that the former may include the fourth centrale or at least have exhibited strong medial growth. The tarsus of *Eoxenopoides* in its general configuration and apparent absence of significant torsion is more primitive than *Xenopus*, and is generally comparable with (e.g.) primitive discoglossids (Vergnaud-Grazzini & Wenz 1975, fig. 5).

The phalanges indicate relatively short fingers. Tinsley (1973) has given ratios for the species of *Xenopus*; the ratio of first finger length/total lower forelimb length in *Eoxenopoides* is 0,45, very close to the result for *X. tropicalis*. The meaning of this is not clear as accurate measurements for other fossil and recent species were not available. Measurements taken from photographs of the Cretaceous *Thoraciliacus* and *Cordicephalus* indicate ratios of about 0,46 for *Thoraciliacus rostriceps* and 0,52 for *Cordicephalus gracilis*. The former thus resembles *Eoxenopoides* and *X. tropicalis*, the latter is closer to the range for the longer-fingered species *X. fraseri* and *X. laevis*. As in *Xenopus* and many other frogs, the third digit is the longest, but in *Eoxenopoides* there is less difference between digit length than in Recent pipids. These proportions are reminiscent of the early Cretaceous pipids from Israel and also of *Palaeobatrachus* spp. as described by Špinar (1972).

The pelvic girdle of *Eoxenopoides* is interesting in that as preserved, the iliac shafts of most specimens extend forward to approach, touch or overlap the transverse processes of the third presacral vertebra. This condition was used by Nevo (1968) as a generic character for the early Cretaceous species of *Thoraciliacus*, not otherwise strongly separated from the sympatric *Cordicephalus*, as Nevo states (Nevo 1968: 272). Whether or not the ilia overlap the ribs has in part to do with the position of the sacrum relative to the ilia at the time of death or shortly thereafter, as well as the position that may be characteristic in life. In general the articulation of the sacrum in forms with narrow sacral diapophyses tends to be at the tip of the ilia (acroiliac of Nevo 1968), and in forms with moderately or widely expanded diapophyses there is of necessity a more posterior articulation (medioiliac of Nevo 1968), the ilia sometimes projecting in front of the sacrum. Nevo has correctly rejected the latter as diagnostic of the 'Eoxenopoididae' of Casamiquela (1961). In the author's experience, specimens of living *Xenopus* that have died as a result of desiccation show an extreme 'medioiliac' condition while those in which the tissues remained moist tend towards an 'acroiliac' condition. The critical factor in deciding the utility of a character state involving overlap of ribs and ilia, then, is the relative length of the ilia as well as the determination of the preferred orientation of the sacrum in life. Considerable movement is possible at the sacroiliac joint (Whiting 1961) so that this latter feature is difficult to assess. Nevo (1968) ascribed a functional significance to the overlap of ilium and transverse process in the forming of a 'synsacrum'. It is doubtful that actual articulation of ilia with ribs occurred and that overlap is of functional significance. In *Xenopus* overlap of transverse processes and ilia may occur (especially in cleared and stained preparations made from desiccated specimens) but in this case neither synsacrum nor joint occurs. There is no evidence that a joint occurred at this overlap in *Eoxenopoides*, nor does it seem that an actual joint can be demonstrated in *Thoraciliacus*. In deposits containing the latter two genera there is no sedimentary evidence that the animals died in burrows (and hence might have dried before final burial by overlying sediments). Nevo (1968) has carefully quantified the differences between the species of *Thoraciliacus* and *Cordicephalus*, and it is not suggested here that only one genus is represented. In *Eoxenopoides reuningi*, however, the overlapping of transverse processes and ilia is not interpreted as demonstrating the presence of a synsacrum: the pattern of variation seen in this species is more easily interpretable as variation in the position of the sacrum relative to the ilia, a pattern of variation that is comparable to that seen in *Xenopus*.

The ossification of the pubis and the development of an iliac symphysis are as in pipids generally. The posterior extent of ischium is relatively great but does not exceed that of other pipids.

The femur and tibiofibula offer no features of comparative interest.

The proximal tarsals (tibiale and fibulare) are fused, as in *Xenopus* and other pipids, and is a fusion that extends beyond the epiphysial caps to the actual cavities of the bones. Neither Trueb (1973) nor Lynch (1973) cited pipids as groups showing fusion of these elements although the synostosis in living forms is quite clear.

The presence of four distinct distal tarsals in *Eoxenopoides* is a primitive condition; so far as the author is aware it is not shown in other frogs, which have the third and fourth distal tarsals fused. The tarsal area as well as the carpus of *Eoxenopoides* thus shows some primitive features.

The presence of a well developed prehallux is primitive and it occurs in *Xenopus* and other pipids. Proportions of the foot are exactly as in *X. muelleri* and *X. laevis*, both of which species have relatively long toes.

The metatarsals and phalanges are notable only in having an extra phalanx in the fifth toe of two out of the three specimens in which the foot is well preserved. The formula of 2–2–3–4–4 is also present in the fossil palaeobatrachid frogs (Špinar 1972) and might be considered a derived character state linking *Eoxenopoides* with the palaeobatrachids. Although pipids and palaeobatrachids are believed to be related (Estes & Reig 1973; Estes 1975*a*) presumably this condition in *Eoxenopoides*, which is lacking in more primitive pipids, is a parallel condition. The presence of the extra phalanx gives no increase in length of the digit when compared with the example having three phalanges in the fifth toe and the significance of the condition cannot be ascertained at this time. Some living frogs increased phalangeal count by developing intercalary cartilages, but these are clearly distinguishable morphologically and functionally from the true phalanges. The case in palaeobatrachids and *Eoxenopoides* is one of true hyperphalangy and appearance and ossification of all phalanges are similar. Utilizing Tinsley's (1973) proportion of tibia length/fifth toe length gives a ratio of about 0,82, almost within the range of the long-limbed *Xenopus laevis* group (ratios of 0,69–0,77, against 0,97–1,12 for the shorter limbed *tropicalis* group, Tinsley 1973).

RELATIONSHIPS OF *EOXENOPOIDES REUNINGI*

From the above comparisons a general assessment of the relationships of *Eoxenopoides reuningi* is not difficult to make. Clearly pipid, it has only two rather weak similarities to the living South American pipids: the lateral position of muscle crests on the frontoparietal, indicating that adductor musculature did not encroach on the dorsal skull table, and the fusion of the first two vertebrae. Neither of these is exclusive to living South American pipids, however; both may occur in species of *Hymenochirus*, and fusion of the first two vertebrae occurs in the fossil *Xenopus romeri* and living *X. tropicalis* as well as in some other groups of frogs (Lynch 1973). No resemblances to *Hymenochirus* exist beyond the skull roof and vertebral configurations commented on above.

There is little resemblance to the Cretaceous fossil pipid *Saltenia ibanezi* from South America. The fragility and general shape of the squamosal and the moderate expansion of sacral diapophyses are the only resemblances to this species, but neither resemblance is significant. Reduction of the squamosal can be achieved independently and the moderate expansion of the sacral diapophyses is probably primitive.

The greatest resemblances of *Eoxenopoides reuningi* lie with species of *Xenopus*. As noted by Estes (1975*a*) understanding of the interrelationships of these species is at a very early stage of development. Tinsley (1973, 1975) has attempted morphological analysis of *Xenopus* based primarily on external features and proportions. Although there are various degrees of intermediacy, he has shown that two informal species groups of *Xenopus* may be recognized. One group has relatively short limbs, fingers and toes and relatively small eyes, and includes *X. vestitus*, *X. gilli* and *X. tropicalis*. The other group has relatively longer limbs, fingers and toes and larger eyes, and includes two groups of related species: *X. clivii* and *X. fraseri* on the one hand, *X. laevis* and *X. muelleri* on the other. To a certain extent the two groups are linked by character states of *X. vestitus*. Tinsley has also suggested the possibility of grouping species of *Xenopus* on the presence of four claws on the foot (*X. fraseri*, *X. clivii* and *X. tropicalis*) or three (the remaining species). It is more likely that the four-clawed condition is primitive and lost in parallel by some members of both groups, or that it is an independently acquired specialization. The adaptive significance of a difference in claw number is not known and the character seems not to display the kind of taxonomic utility expressed by the other states mentioned.

Although there was insufficient osteological material to confirm Tinsley's groupings, the small sample available in this study supports his wide separation of *Xenopus tropicalis* and *X. laevis*, and some of his other conclusions. The skull of *X. tropicalis* is broad and short, with a wide, flattened braincase; that of *X. laevis* is relatively longer and the braincase longer and narrower. In general skull proportions and morphology *X. muelleri* seems least modified among species of *Xenopus*, but in having a relatively long skull shows similarity to *X. laevis*. *X. vestitus* has a wide frontoparietal as in *X. tropicalis*. The position of *X. clivii*, *X. fraseri*, and *X. gilli* is not clarified by the small sample and for the present Tinsley's assessment of their relationships is accepted. The Palaeocene species *X. romeri* from Brazil and the Miocene *X. stromeri* from South West Africa are related to *X. tropicalis* and *X. muelleri* respectively; the affinities of *X. pascuali* from the Eocene of Argentina are now being studied; they may be with *X. muelleri* rather than with the *X. tropicalis* group (Estes 1975*a*).

It remains now to assess the similarities and differences shown by *Eoxenopoides reuningi* to Tinsley's groupings of the species of *Xenopus*. First, there are a group of character states of *E. reuningi* that are probably primitive for pipids in general. These include the nasal shape, anterior position of parietal foramen, narrow cultriform process of parasphenoid, relatively long scapula, configuration of the humerus, primitive carpus (Estes 1975*a*) and the flattened and expanded transverse processes of the posterior vertebrae (Nevo 1968).

A further group of character states emphasizes the distinctiveness of *Eoxenopoides reuningi* when compared with *Xenopus*: these include absence of teeth in the upper jaw, reduction and fusion in the vertebral column, dentary with lateral crest and expanded symphysis, and the combination of relatively short fingers and long toes. With regard to the latter feature the general proportions and length of hind limb and feet closely resemble those of *X. muelleri* and *X. laevis*, but the shortness of the fingers is more as in *X. tropicalis*. The fingers of *E. reuningi* are almost subequal in length, reminiscent of conditions in the Cretaceous pipids from Israel (Nevo 1968) and the palaeobatrachids (Špinar 1972). This combination of character states is found in no other pipid species and seems distinctive enough to justify generic status for *Eoxenopoides*.

There remains for discussion only the group of character states in which *Eoxenopoides reuningi* resembles various species of *Xenopus*. The hemispherical expansions of the inner ear region, in the details of their shape and relationship to the channel for the eustachian tube, are almost precisely duplicated in *Xenopus muelleri* and the fossil South American species *X. romeri* and *X. pascuali* (Estes 1975*a*; Casamiquela 1961) and are lacking in other species of *Xenopus*. Inner ear expansion is found also in the Cretaceous pipids *Thoraciliacus* and *Cordicephalus* from Israel and in the Northern hemisphere palaeobatrachids. Nevo (1968) has noted that this expansion in his material from Israel is positively correlated with size and that it is thus not necessarily a paedomorphic feature. In light of the detailed resemblance of the otic expansion of *E. reuningi* to that of the relatively primitive species of *Xenopus* noted above, this feature may be scored as a rather weak resemblance to these species, although there is definite possibility of parallelism in ear capsule expansion in pipids.

The rhomboidal, toothless shape of the fused vomers closely resembles that of *Xenopus romeri* from the Palaeocene of Brazil and the living species *X. laevis* and *X. clivii*. Fused toothed vomers may occur in *X. muelleri*. The narrow, dorsally channelled shape of the anterior process of the pterygoid is precisely duplicated in all species of *Xenopus*. The shape of this process (if not its far anterior extension, which is found in pipids in general) is a derived feature showing resemblance to all species of *Xenopus*. Presence of an anterior, spoon-shaped process of the maxilla that leads posteriorly into a large, circular foramen is a close resemblance to *X. muelleri* and *X. tropicalis*. As Figure 4 shows, there is perhaps more detailed resemblance of *X. muelleri* and *Eoxenopoides reuningi*. It is interesting that this maxillary configuration is lacking in the more specialized *X. laevis* on the one hand and *X. vestitus* and *X. gilli* on the other, representing both presumed species groups of *Xenopus*. Perhaps this condition is primitive, and like the presence of three or four claws has been lost in parallel in derived species of *Xenopus*.

In summary, there are a number of suggestive resemblances of *Eoxenopoides reuningi* to *Xenopus muelleri* and its possible fossil relative *X. pascuali* on the one hand, and to *X. tropicalis* and its fossil relative *X. romeri* on the other. The similarities of maxilla, ear capsule, and foot proportions to those of *X. muelleri* suggest relationship to this relatively generalized species of *Xenopus*. Indications of resemblance to *X. tropicalis* are weaker and include the broad skull shape, maxillary shape, and fused first two vertebrae; the fused toothless vomer and fusion of first two vertebrae are like those of *X. romeri* (although present in other species as well).

None of the following character states of *Eoxenopoides reuningi* occurs in any living pipid: moderately expanded sacral diapophyses, expanded posterior presacral transverse processes, anterior position of the parietal foramen (the latter also found in the fossil species *X. romeri*, *X. pascuali* and *X. stromeri*), relatively long scapula, and primitive carpus. This probably indicates an early origin of *Eoxenopoides reuningi* relative to the diversification of species of *Xenopus*, in spite of specialization of the former in loss of maxillary teeth and reduction of vertebral number. It is therefore suggested that *Eoxenopoides reuningi* was an early offshoot of a primitive *X. muelleri*-like ancestor of *Xenopus*, a species that included the above-mentioned primitive character states. Presence of these primitive states in *E. reuningi* and their absence (excepting parietal foramen position) in species of *Xenopus* indicates that origin of *E. reuningi* must have been within the Cretaceous to have preceded appearance of *Xenopus*, the origin of which has been estimated as prior to 91 m.y. (Cretaceous, late Turonian; Estes 1975*a*). None of the resemblances of *E. reuningi* to any of the species of *Xenopus* is specific or clear-cut enough to suggest an origin within *Xenopus* although there is a well documented series of character states confirming its close relationship to the living genus, as documented above.

TAPHONOMY AND PALAEOECOLOGY

The specimens of *Eoxenopoides reuningi* occur throughout the sequence of approximately 33 metres of clays forming the deposit, and occur in both black carbonaceous and greenish grey rock types. There was no precise stratigraphic control on the original collection of specimens, many of which came from the dumps around the edge of the pipe. The second collection made by Boonstra had more precise horizon data permitting determination of whether or not the specimen came from high or low in the section. The morphology of the specimens is, however, highly uniform, and no significant variation other than that noted in the text could be detected. More precisely controlled collections may in future demonstrate some stratigraphic progression but the author does not believe that it would achieve or even approach the specific level.

There has been relatively little disarticulation of material; most specimens are relatively well articulated and complete although many have lost parts of the skeleton by breakage in collection. Some maceration occurred, however, as isolated skulls are present and the sediment contains fragments of bones or complete elements from time to time. It is possible that more disarticulated material was originally present but that it was not collected. The excellent condition of preservation of the specimens indicates that after death the specimens were buried rather quickly in conditions that did not permit extensive decomposition. The wide distribution of the specimens throughout the section indicates that no sudden kill was involved although frequent repetitive conditions such as lake overturn could have caused periodic or seasonal kills.

Most of the frog remains were of adult, metamorphosed individuals; only a small number of tadpoles was recovered, all of which were rather late stages with small but well-preserved limbs. The metamorphosed specimens are all well ossified and the individual elements distinctly and completely formed; few indicate specimens that had recently metamorphosed, as far as comparisons with living *Xenopus* permit this to be determined. Size range of the specimens is relatively limited. Total skull width ranges from 6,6 to 10,6 mm, M = 8,8, N = 17, a size close to that of the unmetamorphosed specimens. It is thus probable that *Eoxenopoides reuningi* was either a relatively small species or that all specimens were relatively young and do not indicate maximum size. Wide distribution argues for the former alternative and the author believes that the expressed size range closely matches that of the species.

Close similarity in body proportions to those of living *Xenopus*, particularly the elongated metacarpals and metatarsals and the specialized form of the humerus, indicate that *Eoxenopoides reuningi* was as aquatic as the living *Xenopus* and that its feeding habits were similar, making use of a stereotyped antero-posterior motion of arm and elongated hands to create currents that brought olfactory sensations to the nasal epithelium and to aid in forcing food into the mouth.

What little of the flora is known indicates a relatively dry climate, with rain limited to the warm season (Axelrod 1976 *in litt.*).

ACKNOWLEDGEMENTS

It is a pleasure to acknowledge here the debt that this paper owes to the careful account prepared in 1931 by Dr S. H. Haughton, who correctly placed this interesting fossil frog to family at a time when little of substance on fossil frogs was available in the literature.

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ABBREVIATIONS

C1–4	centralia 1–4
cl	clavicle
cle	cleithrum
co	coracoid
col	columella
d	dentary
D1–4	distal carpals 1–4
fp	frontoparietal
i	intermedium
il	ilium
is	ischium
mx	maxilla
na	nasal
oc	otoccipital
of	optic foramen
p	prepollex or C1
pa	prearticular–articular complex
pas	parasphenoid
pbp	pseudobasal process
pla	planum antorbitale
pmx	premaxilla
pt	pterygoid
pu	pubis
qu	quadrate
r	radiale
ru	radioulna
sc	scapula
sph	sphenethmoid
sq	squamosal
u	ulnare
vo	vomer

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Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

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Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (figs 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

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figures of plates are enclosed in parentheses to distinguish them from text-figures
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In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

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SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33°51′S 25°39′E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

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Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

RICHARD ESTES

RELATIONSHIPS OF THE SOUTH AFRICAN FOSSIL FROG *EOXENOPOIDES REUNINGI* (ANURA, PIPIDAE)

VOLUME 73 PART 3 JUNE 1977 ISSN 0303-2515

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By

HERBERT CHRISTIAN KLINGER
South African Museum, Cape Town

(With 8 figures)

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ABSTRACT

Part of what is believed to have been the Cretaceous outcrop briefly described by Haughton in 1930 was relocated. Mining operations in the area have virtually destroyed the outcrop. Because of its stratigraphic importance, a description and locality data are given for future investigators. The informal term 'Wanderfeld IV' beds is proposed for the Cretaceous (Cenomanian) sedimentary sequence exposed near Bogenfels. The fossils mentioned by Merensky in 1910 from an unknown locality in the Sperrgebiet possibly indicate the presence of Santonian or Campanian sediments. These may be correlated with offshore sediments which have yielded *Sphenoceramus* aff. *S. schmidti*.

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INTRODUCTION

The presence of onshore Cretaceous deposits in South West Africa was first suspected by the discovery and subsequent identification of *Protocardia hillana* (Sowerby), *Turritella bonei* Baily and *Turritella* (*Haustator*) *meadi* Baily by Merensky (1910: 18) in the first decade of this century. The actual locality from which these fossils were collected, however, remains unknown. The first unequivocal evidence for the onshore presence of Upper Cretaceous marine sediments was the fortuitous discovery by Haughton of a shelly bed consisting mainly of *Exogyra* cf. *columba* (= *Rhynchostreon* cf. *suborbiculatum*) and a single ammonite named *Placenticeras merenskyi* sp. nov. (= *Proplacenticeras merenskyi*) in an area well known for abundant Tertiary fossils, previously described by Böhm & Weissermel (1913), Böhm (1926) and Weissermel (1926). The results of the

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discovery were published by Haughton in 1930 (1930*a*: 61–63; 1930*b*: 361–365). Comparison of *Proplacenticeras merenskyi* with placenticeratids from other areas led Haughton to believe that the Bogenfels deposits were 'not earlier than the Lower Senonian' (1930*b*: 364). Unfortunately the locality data given were vague. The Tertiary deposits were described as being 'just to the east and north-east of Wanderfeld IV, north of the old Bogenfels station, and is a small depression running into the Langental', and the Cretaceous deposits as being 'at a spot a few hundred yards to the south' (of the Tertiary outcrops) (Haughton 1930*b*: 362).

Subsequent to Haughton's discovery of the shelly bed and the single ammonite, no one has apparently been able to relocate the Cretaceous outcrop, and doubt has arisen as to whether the Cretaceous fossils were indeed *in situ*, or reworked into the Tertiary sediments, despite Haughton's (1930*b*: 361) adamant rejection of this possibility. One of the reasons why subsequent investigators failed to relocate the outcrop is probably because mining operations have removed virtually all the sediment overlying the bedrock, leaving hundreds of sieved gravel heaps in their place.

Ziegler (1969: 5), having visited the area near Wanderfeld IV, and having examined the single specimen of *Proplacenticeras merenskyi* which is housed in the South African Museum, concluded that 'in view of other palaeo-evidence and the absence of other Ammonites in the section we have to consider it as a reworked specimen'. On the basis of the macro-fauna a Miocene, probably Burdigalian age, was proposed by Ziegler for the sediments outcropping near Wanderfeld IV. The author himself has been quoted as considering the fossils to be remaniè (see Cooper 1974: 88) following an unsuccessful visit to the area in 1970.

During another visit to the area in 1975 with W. G. Siesser the author was fortunate enough to relocate part of what appears to have been the outcrop described by Haughton. In view of the fact that this is the only known marine onshore Cretaceous deposit on the whole west coast of Africa south of Angola, an as accurate as possible locality map and a description of the present conditions of the remains of the outcrop and its relation to the overlying Tertiary sediments are provided.

DESCRIPTION OF LOCALITY AND EXPOSURE

In the sketch map (Fig. 1) compiled from an uncorrected aerial photograph and Kaiser's 1926 map no. 3, Granitberg, the depression running into the Langental is shown due east of Wanderfeld IV (Fig. 2).

Subsequent to Haughton's description of the locality, extensive mining operations were undertaken. The conglomeratic sediments overlying the bedrock were stripped and sieved for diamonds. The area is littered with gravel mounds; the largest concentrations are indicated on the map. In places where the sediment has not been disturbed, the Tertiary fossils occur as typical deflation deposits.

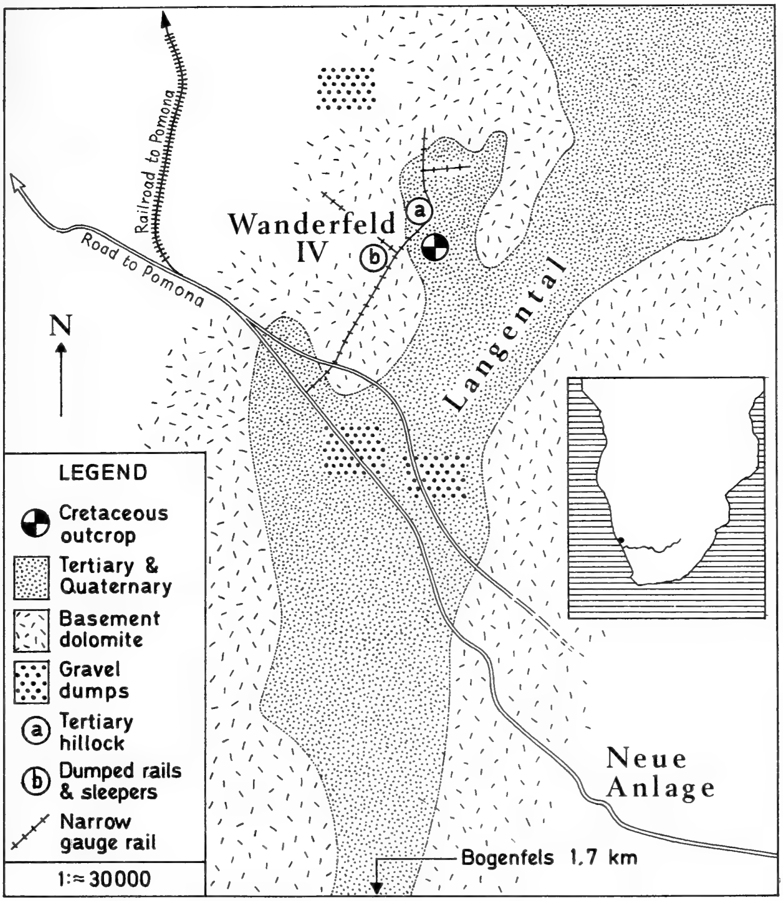


Fig. 1. Sketch map indicating locality of Tertiary and Cretaceous outcrops. (After Kaiser 1926 and uncorrected aerial photograph.)

The surface is littered with rusty-brown turritelid gastropods, heterodont bivalves, ostreids, bryozoans, selachian teeth and occasional specimens of the nautiloid *Aturia lotzei*. An important topographical feature is a low hillock in the western part of the depression (Fig. 3), consisting of green, sandy silts and hard, greyish-white concretionary layers with abundant Tertiary fossils. As this is the only major topographic feature in the depression, both the author and Ziegler here searched in vain for the *Rhynchostreon* bed and incorrectly concluded that the material described by Haughton was probably reworked.

The remains of the Cretaceous outcrop, at 27°23′03″S 15°24′20″E occurs *ca* 70 metres due east of an intersection in the narrow-gauge railroad amidst gravel dumps on the eastern slopes of the depression (Fig. 5). The intersection in the narrow-gauge railroad is marked by dumped rails and sleepers, and is

Fig. 2. View of depression looking north.

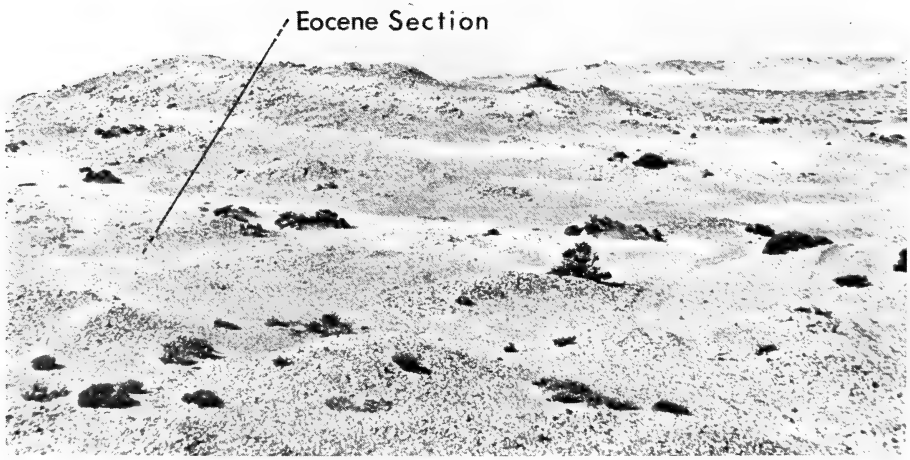


Fig. 3. View of Tertiary hillock in depression. Vehicle tracks on right foreground for scale.

approximately 160 metres south of the Tertiary hillock mentioned above. The remains of the Cretaceous exposure are represented by a few loose concretions, *ca* 20 cm thick, crammed with exogyrans (Figs. 4–5) littering the surface over an area of about 5 m^2. Abundant loose exogyrans occur both on the surface and in the surrounding gravel dumps.

An intensive search in this area for more of this material proved to be negative.

DESCRIPTION OF STRATIGRAPHIC SEQUENCE

The stratigraphic section presented in Figure 6 is very diagrammatic and composite, consisting of the section measured at the Cretaceous locality and also at the Tertiary hillock as shown in Figure 3. Virtually everything is covered by sand at the Cretaceous locality and lack of time and sandstorms made trenching physically impossible. A few shallow pits were dug at suitable places to remove the sand and samples were collected to gain some idea as to the stratigraphic succession. The section at the Tertiary hillock is based on trenching undertaken during 1970. Details of the Tertiary micropalaeontology will be given by W. G. Siesser at a later date.

DISCUSSION OF RESULTS

In situ vs remaniè

In its present condition, only trenching can provide a definite answer to the question of whether the material is reworked or not. According to Haughton (pers. comm.) the outcrop was still intact at the time he and A. L. du Toit had visited the area. Both he and Du Toit were in agreement that the material was definitely not reworked. As to the figured outcrop, the following data favour the concept of the material being *in situ*. According to Haughton (1930*b*: 362), the Tertiary fossiliferous sediments were situated at 70 m above sea-level, and the Cretaceous ones at 60 m. This relationship, as well as the presence of the felspathic grit above the *Rhynchostreon* bed mentioned by Haughton, is also seen in the present description of the stratigraphic sequence. Nearly all the fossils found on the surface show some damage or other due to current sand abrasion, which would be difficult to distinguish from damage due to reworking. The presence of undamaged Cretaceous bivalves in the silty sand underlying the *Rhynchostreon* bed, however, militates against reworking. Furthermore, the lithologies exposed directly above and below the *Rhynchostreon* bed point to low-energy milieu, and it is difficult to envisage large fragments of the shell bed being actively eroded and transported under these conditions.

Tertiary/Cretaceous boundary

The shingle bed described by Haughton (1930*b*: 362) as forming the base of the *Turritella* (Tertiary) beds was not exposed during trenching. The felspathic grit bed exposed above the *Rhynchostreon* (Cretaceous) bed with an apparent

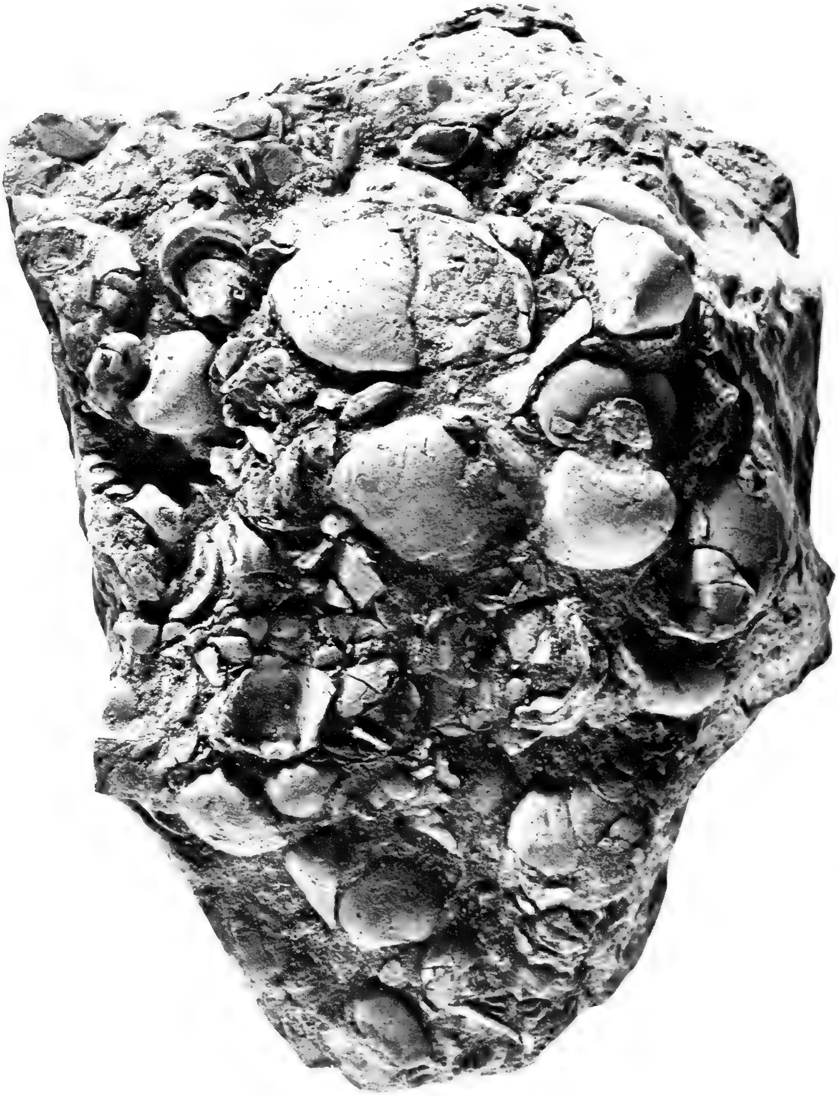


Fig. 4. Loose concretion crammed with *Rhynchostreon suborbiculatum*; ×1.

Fig. 5. View of remains of Cretaceous exposure amidst rubble heaps. Prospecting shovel on right for scale.

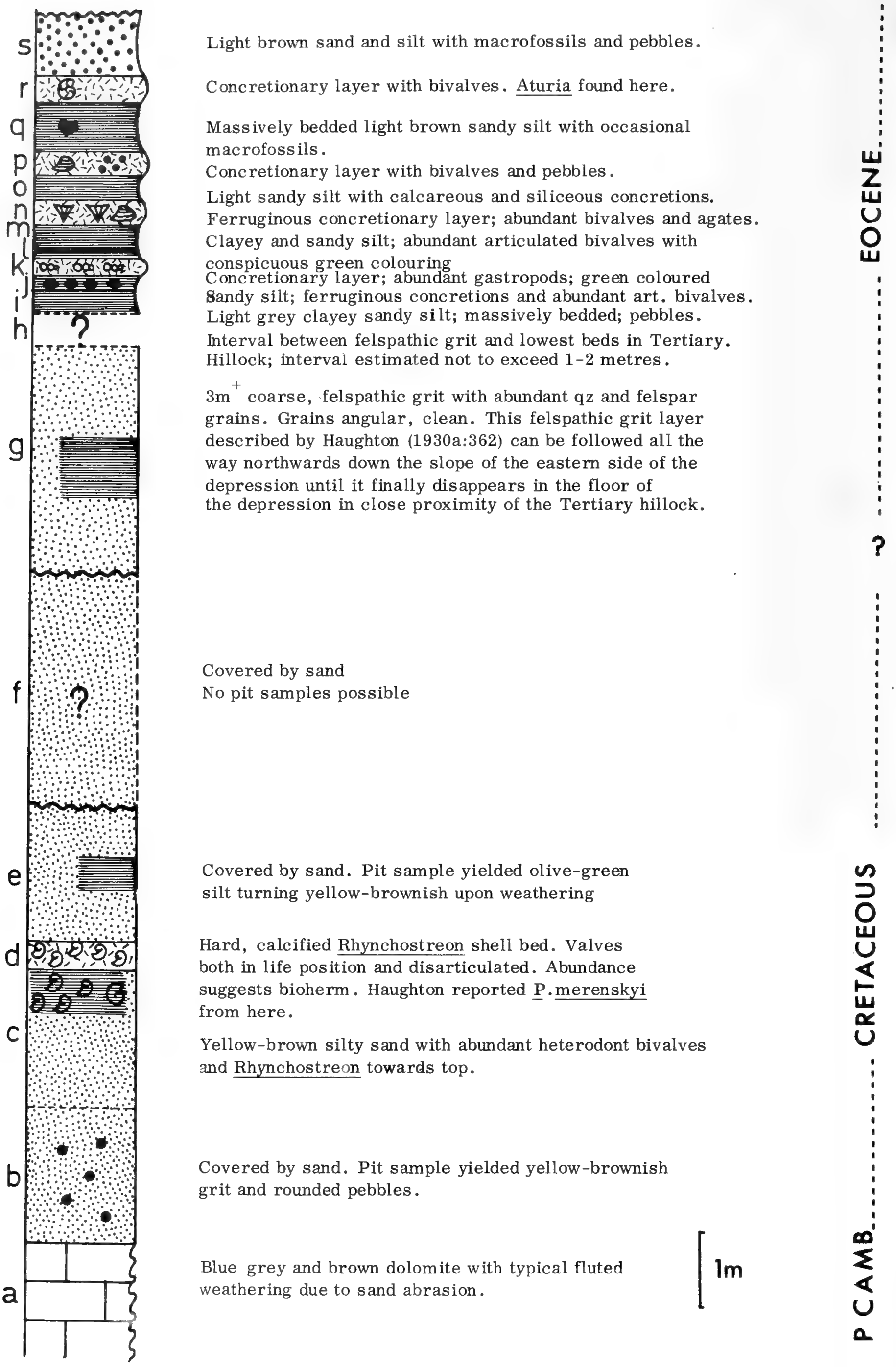
dip towards the north-east could, however, be followed all along the eastern slopes of the depression up to a short distance from the first outcrops of fossiliferous Tertiary sediments. Whether the felspathic grit forms the base of the Tertiary or represents termination of Cretaceous sedimentation is not known. Micropalaeontological samples proved to be of no assistance in this matter. The boundary between the Cretaceous and Tertiary systems is between beds (e) and (i) in the section.

Age of Cretaceous sediments

Micropalaeontological samples taken directly above and below the *Rhynchostreon* bed were either barren or contained poorly preserved non-diagnostic or unidentifiable micro-faunas. Subsequent to Haughton's discovery of the locality, no new faunal elements have been found here. The only indicators of age are *Proplacenticeras merenskyi*, here refigured as Figure 7, and *Rhynchostreon suborbiculatum* (Fig. 8A–G).

On the assumption that the group of placenticeratids, to which *P. merenskyi* belongs, did not occur earlier than the Coniacian, Haughton (1930*b*: 364) concluded that it would not be possible to place the age of these deposits 'any earlier than the Lower Senonian'. Dingle (1973: 346) tentatively substantiated this and postulated that these deposits could possibly represent the base of the unconformity developed in south-eastern Africa described by Kennedy & Klinger (1971). On the basis of the occurrence of *Rhynchostreon* cf. *suborbiculatum* in the uppermost Cenomanian of Salinas, southern Angola, Cooper (1974: 87–8) suggests a Late Cenomanian age for the Bogenfels deposits.

Proplacenticeras generally has a time range of Cenomanian to Coniacian



Light brown sand and silt with macrofossils and pebbles.

Concretionary layer with bivalves. Aturia found here.

Massively bedded light brown sandy silt with occasional macrofossils.

Concretionary layer with bivalves and pebbles.

Light sandy silt with calcareous and siliceous concretions.

Ferruginous concretionary layer; abundant bivalves and agates.

Clayey and sandy silt; abundant articulated bivalves with conspicuous green colouring

Concretionary layer; abundant gastropods; green coloured

Sandy silt; ferruginous concretions and abundant art. bivalves.

Light grey clayey sandy silt; massively bedded; pebbles.

Interval between felspathic grit and lowest beds in Tertiary. Hillock; interval estimated not to exceed 1-2 metres.

3m$^+$ coarse, felspathic grit with abundant qz and felspar grains. Grains angular, clean. This felspathic grit layer described by Haughton (1930a:362) can be followed all the way northwards down the slope of the eastern side of the depression until it finally disappears in the floor of the depression in close proximity of the Tertiary hillock.

Covered by sand
No pit samples possible

Covered by sand. Pit sample yielded olive-green silt turning yellow-brownish upon weathering

Hard, calcified Rhynchostreon shell bed. Valves both in life position and disarticulated. Abundance suggests bioherm. Haughton reported P. merenskyi from here.

Yellow-brown silty sand with abundant heterodont bivalves and Rhynchostreon towards top.

Covered by sand. Pit sample yielded yellow-brownish grit and rounded pebbles.

Blue grey and brown dolomite with typical fluted weathering due to sand abrasion.

Fig. 6. Diagrammatic section of Cretaceous and Tertiary exposure near Bogenfels.

Fig. 7. SAM–10569 *Proplacenticeras merenskyi* (Haughton). Holotype; ×1.

(Wright 1957: L390), but may occur as early as the Upper Albian (see Collignon 1963: 126). *Rhynchostreon* is generally restricted to the Cenomanian and Turonian (Stenzel 1971: N1123–4). It is suspected, however, that typical forms of *R. suborbiculatum*, such as these found near Bogenfels, are restricted to the Early and Middle Cenomanian throughout the world. As Haughton states that the *P. merenskyi* specimen was found in the *Rhynchostreon* bed, the possibility that more than one age is represented may be excluded. The concurrent range zone of these two species thus suggests a Cenomanian age for the *Rhynchostreon* shell beds near Bogenfels.

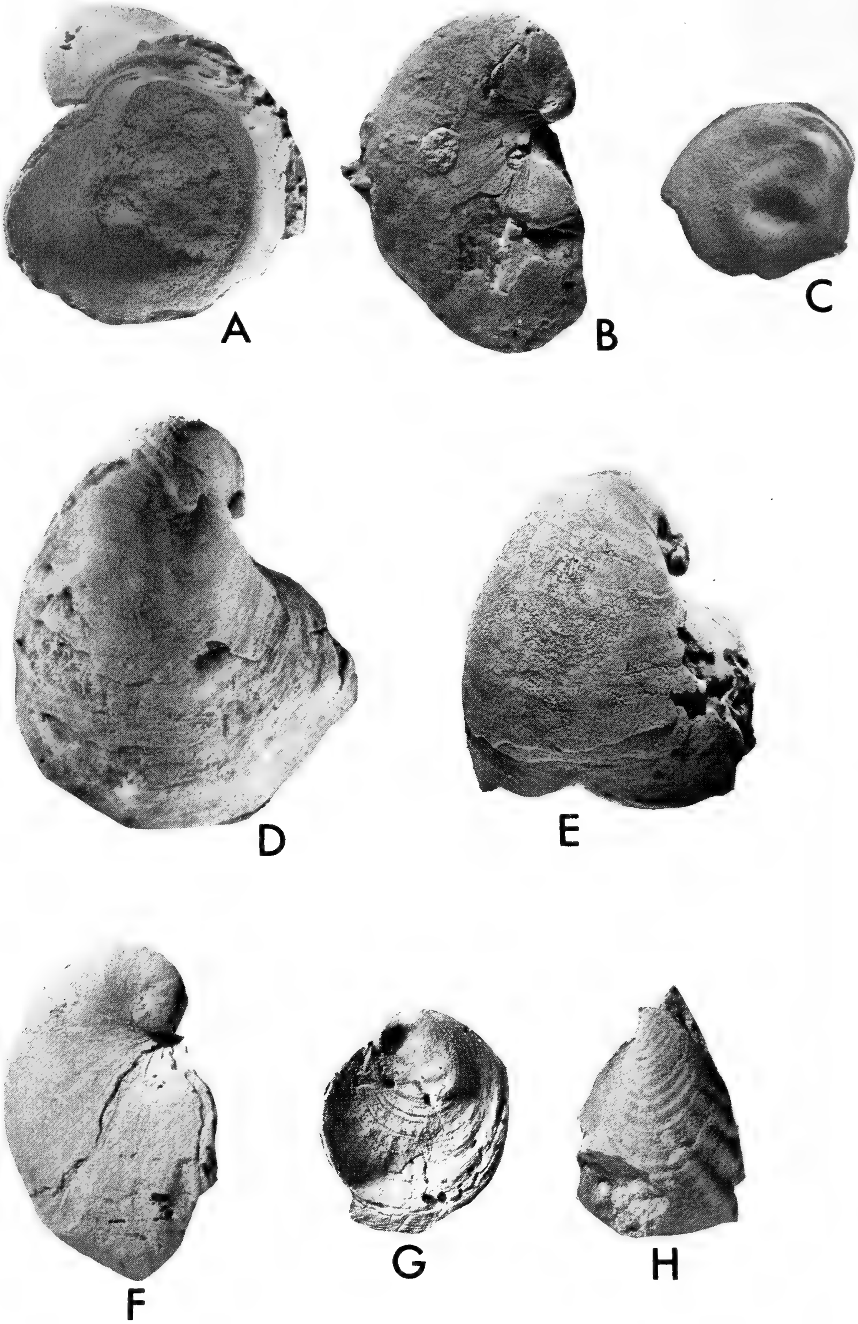


Fig. 8. A–G. *Rhynchostreon suborbiculatum.* Specimens SAM–PCS5498–5503. A–C, F–G natural size. D–E ×1,2. H. *Sphenoceramus* aff. *S. schmidti.* SAM–PCS5504; ×1.

At this stage comments on the fossils mentioned by Merensky seem opportune. The locality from which these fossils were obtained is unknown, as Merensky did not collect them himself, but obtained them from Mr Schettler, a representative of the Koloniale Gesellschaft. According to Haughton (1930*b*: 361) the Tertiary exposure near Bogenfels was shown to Schettler, but it is unknown if the fossils were indeed collected there. According to Merensky (1910: 18), 'News of further finds (diamonds) which were made . . . opposite Plumpudding island, arrived shortly before my departure, so that I could not visit them. Mr. Schettler . . . having just returned from this locality, showed me samples from these.' Reference to Plumpudding Island suggests a locality in the vicinity of Kakaoberg or Buntfeldschuh, south of Bogenfels.

These fossils could not be traced, and Merensky's identifications receive the benefit of the doubt. Merensky assumed that the fossils identified by him were of the same age as the fauna from the Umzamba Formation. If this assumption is correct, an age of Middle Santonian to Early Campanian can be assigned to these fossils (Klinger & Kennedy 1977). Cooper suggests a Santonian age on the basis of the fossils identified by Merensky.

To date, no other fossils have been found to either confirm or negate the existence of these 'hypothetical' Santonian/Campanian deposits. Offshore drilling at 28°23′S 15°25′E yielded a single specimen of a juvenile inoceramid, tentatively identified as *Sphenoceramus* aff. *S. schmidti* (Fig. 8H). The latter seems to indicate a Middle Santonian to Late Campanian age for the offshore exposures. Being of the same age, the offshore deposits could possibly be the equivalents of the onshore deposits which allegedly yielded the fauna identified by Merensky.

Nomenclatorial status of Cretaceous deposits

As the outcrop at Wanderfeld IV is not, at present, a mapable unit, it is suggested that it should retain informal status as the 'Wanderfeld IV beds' until similar lithologies are found onshore or offshore.

ACKNOWLEDGEMENTS

The author wishes to express his gratitude to Dr C. Stocken, Mr R. Little and Mr D. Minney of Consolidated Diamond Mines of South West Africa for their generous assistance without which field work would have been impossible. Dr W. G. Siesser of the Marine Geoscience Unit of the University of Cape Town organized the 1975 excursion and his invitation to join him in this venture is gratefully acknowledged. Thanks are due to Dr S. H. Haughton for his comments on the locality and the outcrop. Dr E. G. Kauffman (Washington) kindly identified the exogyrans and the inoceramid; the latter was donated by Mr R. Joynt of the Marine Diamond Corporation. Dr H. de la R. Winter of SOEKOR gave permission for parts of Ziegler's unpublished report to be quoted, for which the author is grateful. Mr C. Hunter and Mr V. Branco kindly assisted with the illustrations.

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Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

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Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (figs 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:
comma separates author's name and year
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full stop separates references by different authors
figures of plates are enclosed in parentheses to distinguish them from text-figures
dash, not comma, separates consecutive numbers

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In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33°51′S 25°39′E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

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(a) The Figures, Maps and Tables of the paper when referred to in the text
e.g. '. . . the Figure depicting *C. namacolus* . . .'; '. . . in *C. namacolus* (Fig. 10) . . .'

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HERBERT CHRISTIAN KLINGER

CRETACEOUS DEPOSITS NEAR BOGENFELS, SOUTH WEST AFRICA

VOLUME 73 PART 4 JUNE 1977 ISSN 0303-2515

ANNALS
OF THE SOUTH AFRICAN MUSEUM

CAPE TOWN

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Address(es) of author(s) (institution where work was carried out)
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(c) *Table of contents* giving hierarchy of headings and subheadings
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(e) *Subject-matter* of the paper, divided into sections to correspond with those given in table of contents
(f) *Summary*, if paper is lengthy
(g) *Acknowledgements*
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Footnotes should be avoided unless they are short and essential.

Only generic and specific names should be underlined to indicate italics; all other marking up should be left to editor and publisher.

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All illustrations, whether line drawings or photographs, should be termed figures (plates are not printed; half-tones will appear in their proper place in the text) and numbered in a single series. Items of composite figures should be designated by capital letters; lettering of figures is not set in type and should be in lower-case letters.

The number of the figure should be lightly marked in pencil on the back of each illustration.

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(*continued inside back cover*)

ANNALS OF THE SOUTH AFRICAN MUSEUM
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DEEP-SEA AMPHIPODS FROM WEST OF CAPE POINT, SOUTH AFRICA

By

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Cape Town Kaapstad

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DEEP-SEA AMPHIPODS FROM WEST OF CAPE POINT, SOUTH AFRICA

By

CHARLES L. GRIFFITHS

Institute of Oceanography, University of Cape Town

(With 6 figures)

[*MS. accepted 26 January 1977*]

ABSTRACT

Two new species, *Euonyx scutatus* sp. nov. and *Epimeria concordia* sp. nov., are described from this small collection, while of the remaining five species four are recorded for only the second time and are new to southern African waters.

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INTRODUCTION

Although the amphipods of shallower waters around South Africa are relatively well documented, very few records exist from depths exceeding 1 000 m. The first significant series of such samples was that collected by the S.S. *Pieter Faure* between 1879 and 1907, from the vicinity of the Cape of Good Hope, and described by K. H. Barnard (1916, 1925). Since that time only occasional, widely scattered samples of deep-sea amphipods have been reported from the region, notable amongst these being the collections of the *Galathea* expedition (J. L. Barnard 1961) and the R.V. *Vema* cruises (J. L. Barnard 1962*b*).

The present material is derived from twelve samples collected by Dr F. H. Talbot of the South African Museum on board the R.S. *Africana II*, during August and December 1959. An Agassiz trawl of approximately 1 cm mesh was used and the area sampled was adjacent to, but somewhat deeper than, that explored by the S.S. *Pieter Faure*. Due to the large size of mesh used only a few relatively large amphipods were recovered, but these are of considerable interest as they include two species new to science and four others new to the region. All the specimens have been deposited in the South African Museum, Cape Town.

Ann. S. Afr. Mus. 73 (4), 1977: 93–104, 6 figs.

DESCRIPTION OF MATERIAL

Suborder GAMMARIDEA

Family **Dexaminidae**

Lepechinella (?) *sucia* J. L. Barnard, 1961

Fig. 1

Lepechinella sucia J. L. Barnard, 1961: 99, fig. 69.

Records

SAM–A13653, 33°49′S 16°30′E, 2 700 m, 27 August 1959, 3 males, 8 females.

Remarks

The degree of intraspecific variation amongst members of this exclusively abyssal genus is poorly understood, since many species are known from only a few individuals. The present material shows a close affinity to the unique male of *L. sucia* recorded from the Tasman Sea by J. L. Barnard (1961). The present specimens show more general setation than the Tasmanian individual, but lack its distinct lateral rows of setae on first and second pleonal epimera. The resemblance as regards other significant features, such as shapes of the coxae and pereonal teeth, is, however, so close that separation of the two forms seems unjustified, at least until intraspecific stability of setation patterns is better understood. To facilitate comparison figures of a typical South African male are provided.

Distribution

Tasman Sea, (?) South Africa.

Family **Ischyroceridae**

Bathyphotis tridentata Stephensen, 1944

Fig. 2

Bathyphotis tridentata Stephensen, 1944: 26, figs 17, 18.

Records

SAM A–13656, 34°49′S 16°30′E, 2 700 m, 27 August 1959, a single male.

Remarks

There can be no doubt that the present specimen is synonymous with that described by Stephensen, since there are only minor quantitative differences in the characteristic forms of gnathopod 2, pereiopod 3 and pleon segment 4.

There are, however, some points of difference which are a considerable taxonomic significance. Stephensen noted a paucity of spines on maxilla 1 of his

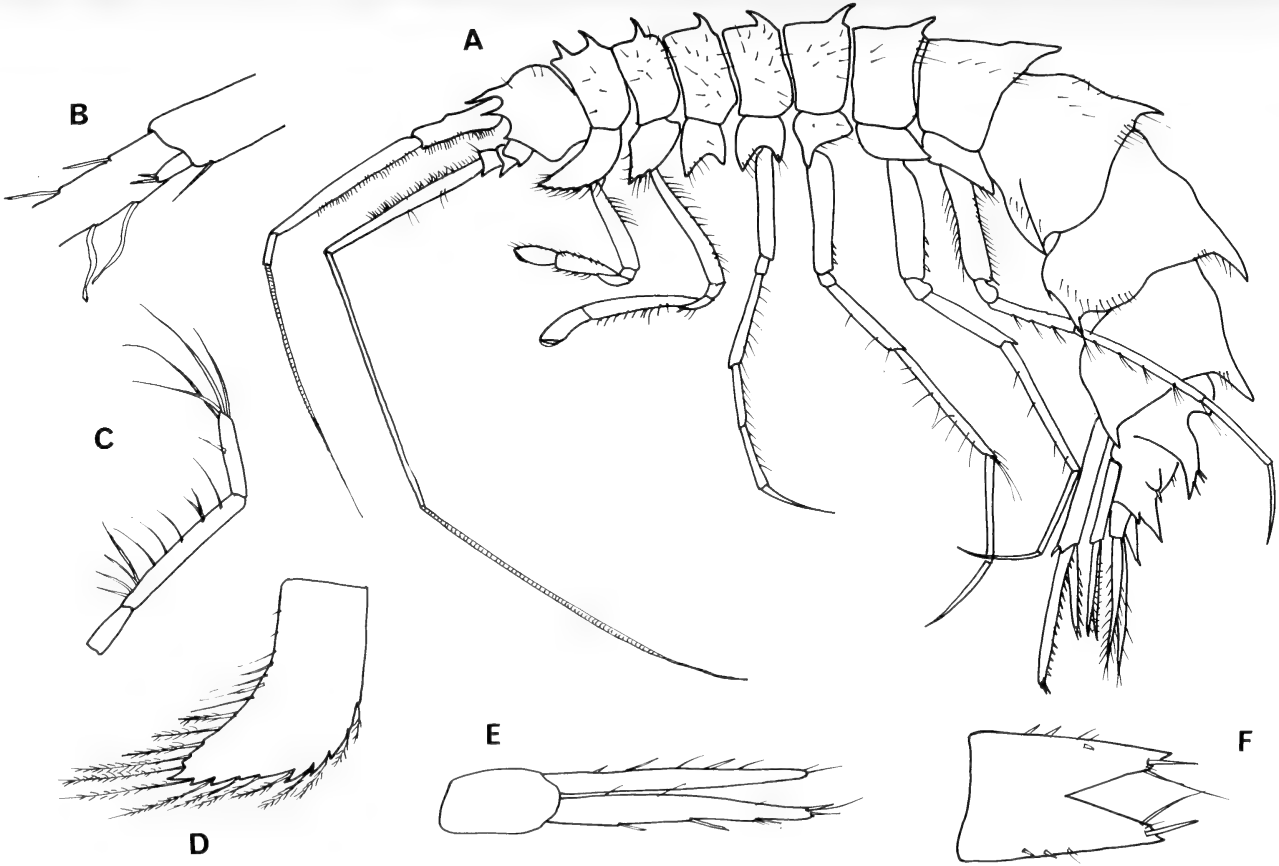

Fig. 1. *Lepechinella* (?) *sucia* J. L. Barnard, 1961.

Male, 13 mm. A. Lateral aspect. B. Accessory flagellum. C. Mandibular palp. D. Coxa 1. E. Uropod 3. F. Telson.

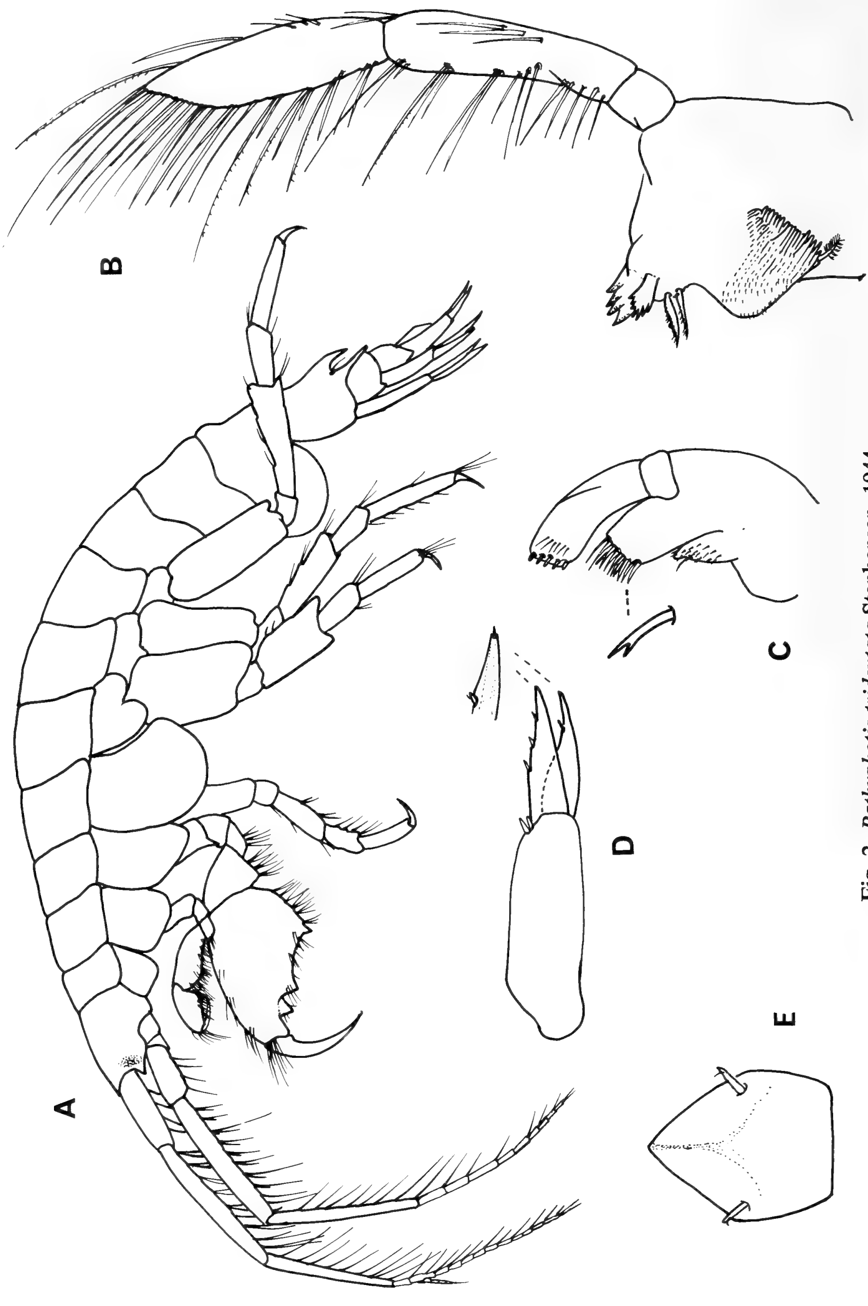

Fig. 2. *Bathyphotis tridentata* Stephensen, 1944.
A. Lateral aspect. B. Mandible. C. Maxilla 1. D. Uropod 3. E. Telson.

specimen (4 on outer plate, 3 on palp), a feature which he considered generically significant. Careful dissection of the present male shows a more usual figure of ten spines on the outer plate and five on the palp (some of the spines shown by Stephensen were broken, indicating that the maxilla may have suffered some damage, hence his low spine count).

Stephensen placed his material close to *Eurystheus* (= *Gammaropsis*), but the species has subsequently been removed to Ischyroceridae (J. L. Barnard 1962*a*) and the structure of uropod 3 has since come to be regarded as '. . . with elongate peduncle, rami short . . . outer ramus hooked apically' (J. L. Barnard 1973). In his original description Stephensen makes no mention of a hooked outer ramus, although such a feature could possibly be inferred from his figure 18. Rather, he described the rami as '. . . narrow, acute, equal in length and breadth'—a description consistent with present observation, although the rami show a minute immersed apical spine when viewed under high-power magnification.

From the above evidence it would appear that the genus *Bathyphotis* is not as discreet, nor as typically 'ischyrocerid', as has come to be supposed, although the excavate coxa 4 remains unique amongst both Corophiidae and Ischyroceridae. The placement of the genus remains open to question and a decision should perhaps await a definitive revision of the entire group. In particular, the importance of shortening of rami of uropod 3 and the significance of this factor relative to uncination of the outer ramus await clarification. An extensive discussion of the utilization of these and other features is given by J. L. Barnard (1962*a*), whose *Eurystheus ventosa*, for example, is closely allied to *Bathyphotis* (especially considering the revised description of maxilla 1 herein). *E. ventosa* has recently been made the type of a new genus *Ventojassa* J. L. Barnard, 1970, and transferred to Ischyroceridae. However, both this genus, *Bathyphotis* and *Microjassa* have third uropods tending to merge with the condition found in Corophiidae.

Family **Lysianassidae**

Eurythenes gryllus (Lichtenstein, 1822)

Eurythenes gryllus: J. L. Barnard, 1961: 35, figs 5–7.

Records

SAM–A13653, 34°42′S 16°54′E, 3 200 m, 8 December 1959, a single female, 30 mm.

Remarks

Closely resembles the female figured by J. L. Barnard (1961). May be distinguished from *E. obesus* by the larger article 2 of pereiopods 3–5 and shorter dactyl of the same limbs.

Distribution

Atlantic and North Pacific.

Euonyx scutatus sp. nov.

Fig. 3

Description (of female, 16 mm)

Head shorter than pereon segment 1, ocular lobes acute, eyes absent; flagellum of antenna 1 of one long and eighteen short articles, accessory flagellum of nine articles; antenna 2 half as long again as 1, flagellum of thirty-seven articles; epistome not projecting anteriorly, only slightly sinuous; mandibular molar a large plate with raised margins, incisor simple, palp 3-articulate; palp of maxilla 1 bi-articulate, outer plate with ten strong serrate spines, inner plate bearing three plumose setae; outer plate of maxilliped excavate medio-distally.

Pereon dorsally carinate, segments 5–7 with progressively more pronounced posterior teeth; coxa 1 triangular, gnathopod 1 chelate, articles 5 and 6 subequal in length; palm of gnathopod 2 straight, transverse; coxa 5 developed into a conical hump, other coxae normal; article 4 of pereiopods 3–5 strongly expanded and distally produced.

Pleon segments 1–3 carinate, bearing postero-dorsal teeth, pleon segment 4 with a conical posterior hump; first pleonal epimeron smoothly rounded, 2 and 3 more quadrate; rami of uropod 1 lanceolate, 2 with outer ramus 80 per cent length of inner; uropod 3 with inner ramus apically truncated, outer ramus lanceolate, slightly the longer; telson 80 per cent cleft.

Holotype

SAM–A13652, female, 16 mm; unique.

Type locality

34°37′S 17°03′E, 2 900 m, 8 December 1959.

Relationships

Although some other species of *Euonyx* (*E. chelatus*, *E. conicurus*) show a dorsal tooth on pleon segment 4, no others have the extensive series of pereonal and pleonal teeth found in *E. scutatus* sp. nov. This species is also distinguished by its triangular coxa 1 and shield-like coxa 5 as well as by details of the structure of gnathopod 2.

Lepidepecreoides nubifer J. L. Barnard, 1971

Fig. 4

Lepidepecreoides nubifer J. L. Barnard, 1971: 41, figs 26–27.

Records

SAM–A10547, 34°36′S 17°00′E, 2 740 m, 10 December 1959.

Remarks

This is only the second record of this species and the first of a female. The specimen closely resembles the smaller male described by J. L. Barnard (1971),

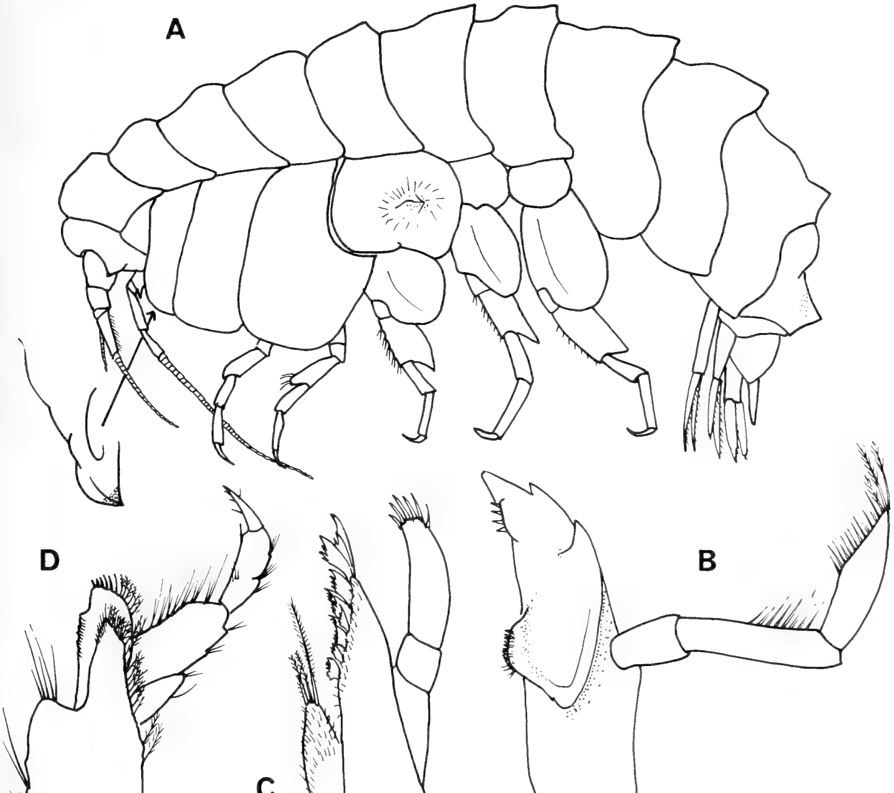

Fig. 3. *Euonyx scutatus* sp. nov.

Female, 16 mm. A. Lateral aspect with epistome enlarged. B. Mandible. C. Maxilla 1. D. Maxilliped. E–F. Gnathopods 1, 2. G. Uropod 3. H. Telson.

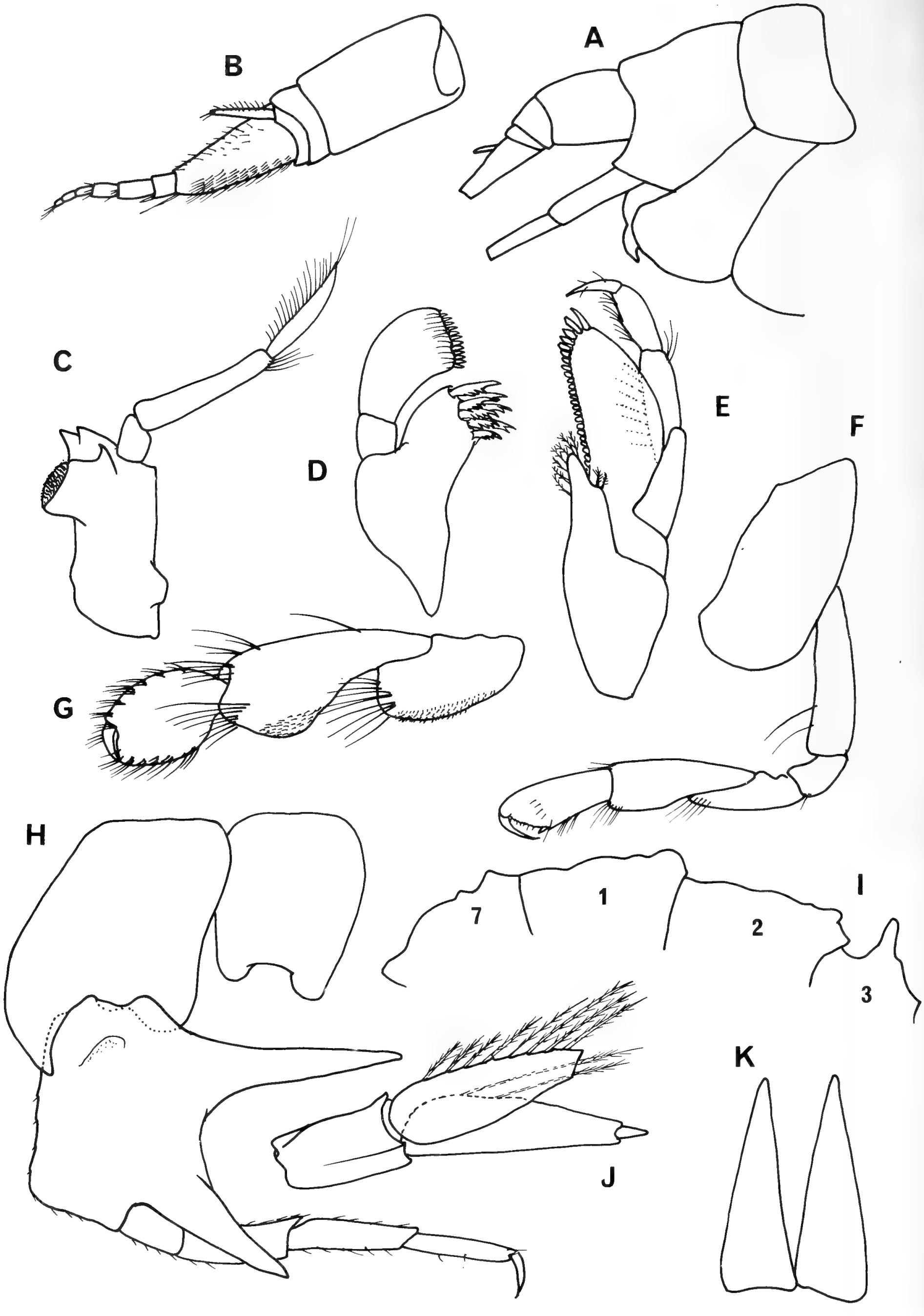

Fig. 4. *Lepidepecreoides nubifer* J. L. Barnard, 1971.

Female, 17 mm. A. Head. B. Antenna 1. C. Mandible. D. Maxilla 1. E. Maxilliped. F–G. Gnathopods 1, 2. H. Pereiopod 3. I. Dorsal profile of pereon segment 7 and pleon. J. Uropod 3. K. Telson.

except for its more tubercular dorsal profile and the longer processes of article 2 of pereiopod 3. Variability of dorsal profile may be a factor of size or sex, but at present cannot be regarded as taxonomically significant. Variations in the lengths of the processes of article 2 of pereiopod 3 are documented for the type species of the genus, *L. xenopus* K. H. Barnard, although in this case the processes were longer in smaller individuals.

Distribution

Oregon 2 860 m, South Africa 2 740 m.

Family **Paramphithoidae**

Epimeria concordia sp. nov.

Fig. 5

Description (of female, 30 mm)

Rostrum elongate, reaching tip of article 3 of antenna 1, head with distinct ocular bulge; pereon segments dorsally smooth, except for small posterior hump on segment 7; article 6 of gnathopod 1 widening slightly, posterior margin with six equally spaced slender spines, palm straight, almost transverse, defined by a single slender spine, dactyl serrate; gnathopod 2 similar to 1 but palm defined by two spines; coxa 4 with long anteroventrally curved cusp and oblique ridge; coxa 5 strongly produced laterally, forming a large triangular 'wing' when viewed from above; coxa 6 with a much smaller lateral process; coxa 7 coniform; article 2 of pereiopod 5 proximally dilated.

Pleon segments 1–3 each with a large upright mediodorsal tooth, segment 4 with a quadrate notch basally and small erect tooth posteriorly; pleonal epimera with accessory tooth on posterior margin, postero-distally acute, second epimeron with an oblique ridge; uropods lanceolate, projecting equally; telson distinctly emarginate apically.

Holotype

SAM–A13651, female, 30 mm, unique.

Type locality

34°36′S 17°00′E, depth 2 740 m, 10 December 1959.

Relationships

This species is remarkable for the enlarged lateral projection of coxa 5, which readily distinguishes it from other species occurring in southern Africa. In other respects it is similar to the closely related group comprising *E. glaucosa* J. L. Barnard, *E. cora* J. L. Barnard, *E. subcarinata* Nagata and *E. pacifica* Gurjanova. None of these forms, however, exhibit the combination of elongate rostrum, large pleonal teeth and accessory teeth on the pleonal epimera, as found in *E. concordia* sp. nov.

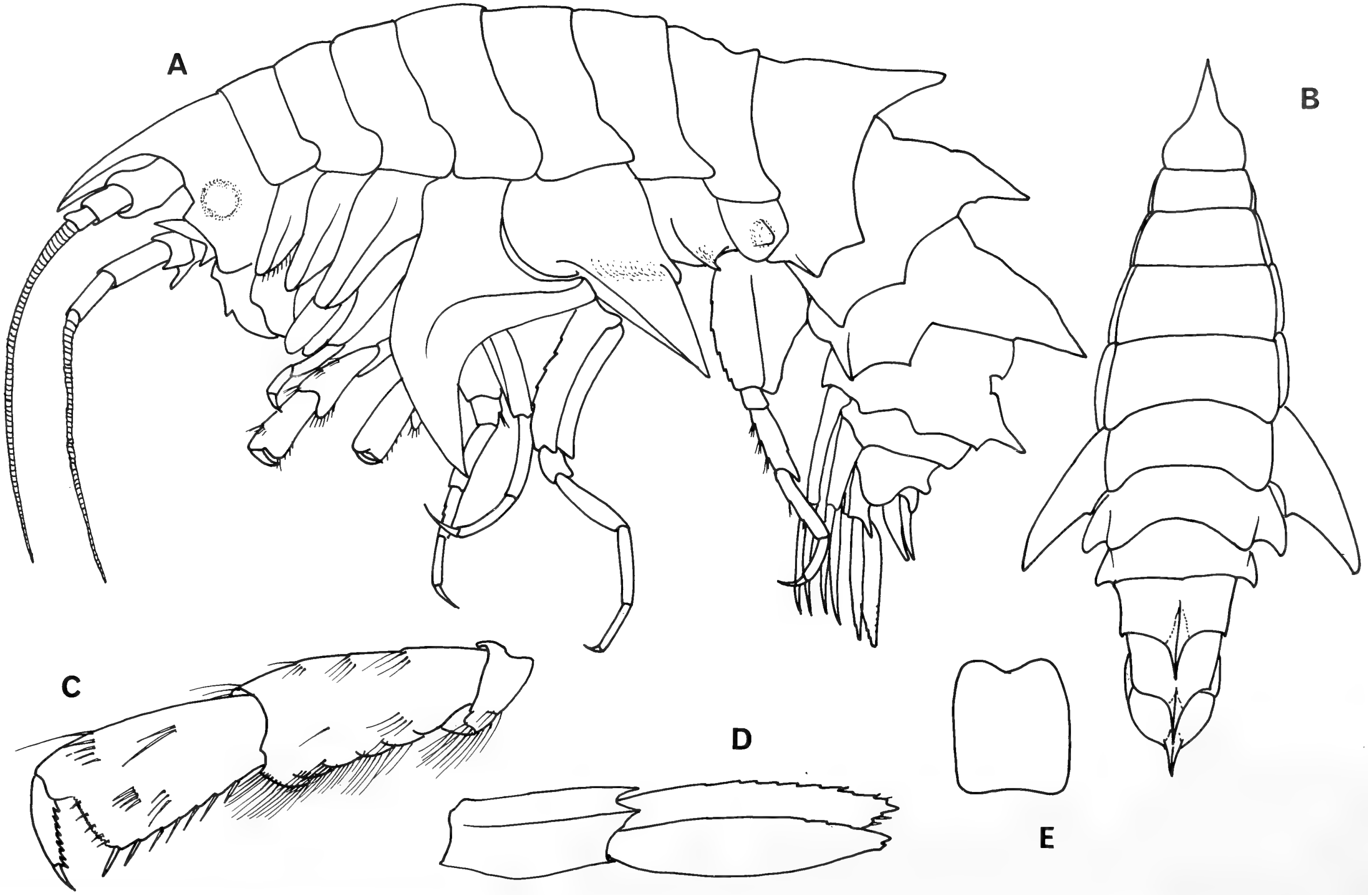

Fig. 5. *Epimeria concordia* sp. nov.

Female, 30 mm. A. Lateral aspect. B. Dorsal aspect. C. Gnathopod 1. D. Uropod 3. E. Telson.

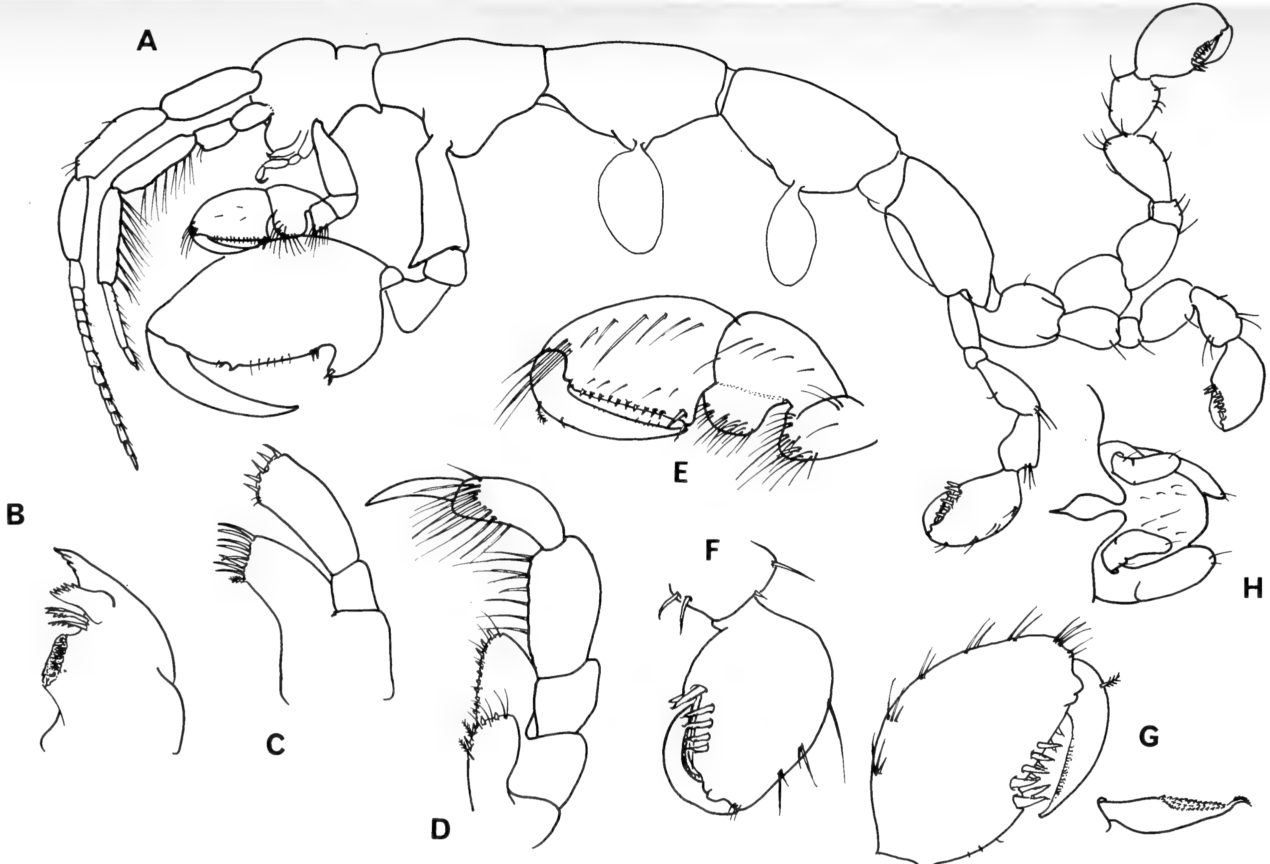

Fig. 6. *Caprella ungulina* Mayer, 1903.

Male, 10 mm. A. Lateral aspect. B. Right mandible. C. Maxilla 1. D. Maxilliped. E. Gnathopod 1. F–G. Articles 6 and 7 of pereiopods 3, 5. H. Abdomen.

Suborder CAPRELLIDEA

Family **Caprellidae**

Caprella ungulina Mayer, 1903

Fig. 6

Caprella ungulina Mayer, 1903: 127, pl. 5 (fig. 36), pl. 8 (figs 30–31).

Records

33°50′S 17°21′E, 1 100 m, 25 August 1959, numerous males and juveniles attached to appendages of the giant stone crab *Neolithoides asperrimus* K. H. Barnard.

Remarks

One of the few caprellids occurring below 1 000 m, readily identified by the strong spines on the palms of pereiopods 5–7. This species has not been recorded since its original description in 1903, hence Mayer's somewhat rudimentary figures are supplemented here.

Distribution

West coast of North and South America; South Africa (Mayer does not state whether his material was found in association with stone crabs, as was the case with the present specimens).

ACKNOWLEDGEMENTS

The author is indebted to the South African Museum for the loan of material upon which this work was based and for the provision of library facilities. Financial support was provided by the South African Council for Scientific and Industrial Research. The manuscript was kindly typed by Mrs S. Hardman.

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6. SYSTEMATIC papers must conform with the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

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Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (figs 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

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Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33°51′S 25°39′E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

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(a) The Figures, Maps and Tables of the paper when referred to in the text
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Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

CHARLES L. GRIFFITHS

DEEP-SEA AMPHIPODS FROM WEST OF CAPE POINT, SOUTH AFRICA

VOLUME 73 PART 5 JUNE 1977 ISSN 0303-2515

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THE SOUTH AFRICAN MUSEUM'S *MEIRING NAUDE* CRUISES
PART 3
HYDROIDA

By

N. A. H. MILLARD

Cape Town Kaapstad

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THE SOUTH AFRICAN MUSEUM'S *MEIRING NAUDE* CRUISES

PART 3

HYDROIDA

By

N. A. H. Millard

South African Museum, Cape Town

(With 10 figures and 1 table)

[*MS. accepted 2 February 1977*]

ABSTRACT

The paper describes a collection of hydroids from off the east coast of South Africa, most of them from depths of over 500 m. In all there are 34 species, of which 8 are new records for the country. Among the latter are 1 new genus—*Uniscyphus*—and 3 new species—*Cladocarpus natalensis*, *Uniscyphus fragilis* and *Zygophylax inconstans.*

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INTRODUCTION

The hydroids described in this paper were dredged off the coast of Natal during two cruises of the R.V. *Meiring Naude* undertaken by the Marine Biology Department of the South African Museum during May 1975 and May 1976. The Station Data for these two cruises were given in an earlier number of this journal (Louw 1977) and will not be repeated here.

The depths of the samples varied from 40 to 1 200 m; most of them were over 500 m, so that these samples were from well over the edge of the continental shelf at 200–400 m, an area which is poorly known and where little collecting has been done.

Ann. S. Afr. Mus. **73** (5), 1977: 105–131, 10 figs, 1 table.

LIST OF SPECIES

* New records for South Africa
† Discussed further in the following pages

	Station number	*South African Museum number*
Family **Bougainvilliidae**		
*†*Garveia crassa* (Stechow, 1923)	SM 58	SAM–H2875
	SM 66	SAM–H2876
Family **Campanulinidae**		
*†*Egmundella ?superba* Stechow, 1921	SM 38	SAM–H1967
Modeeria rotunda (Quoy & Gaimard, 1827)	SM 23	SAM–H1963
	SM 86	SAM–H2808
†*Opercularella* sp.	SM 38	SAM–H1969
	SM 103	SAM–H2854
*†*Stegolaria geniculata* (Allman, 1888)	SM 38	SAM–H1968
Family **Haleciidae**		
Halecium tenellum Hincks, 1861	SM 92	SAM–H2812
	SM 103	SAM–H2858
Family **Lafoeidae**		
Acryptolaria conferta (Allman, 1877)	SM 15	SAM–H1952
	SM 23	–
	SM 86	SAM–H2807
	SM 94	SAM–H2847
	SM 103	SAM–H2852
	SM 107	SAM–H2856
Acryptolaria rectangularis (Jarvis, 1922)	SM 15	–
	SM 16	SAM–H1953
	SM 23	SAM–H1957
	SM 86	SAM–H2805
	SM 94	SAM–H2848
	SM 107	–
Filellum serratum (Clarke, 1879)	SM 38	SAM–H1978
	SM 43	–
†*Lafoea dumosa* (Fleming, 1820)	SM 23	SAM–H1958
	SM 38	SAM–H1965
	SM 67	SAM–H2801
	SM 86	SAM–H2871
	SM 92	SAM–H2811
	SM 99	SAM–H2849
	SM 103	SAM–H2851
Zygophylax africana Stechow, 1923	SM 23	SAM–H1973
	SM 86	SAM–H2806
	SM 92	–
*†*Zygophylax brownei* Billard, 1924	SM 23	SAM–H1974
	SM 86	SAM–H2874
*†*Zygophylax inconstans* sp. nov.	SM 23	SAM–H1975
	SM 43	SAM–H1977
Zygophylax sibogae Billard, 1918	SM 23	SAM–H1956
	SM 31	SAM–H1964
	SM 52	SAM–H2800
	SM 86	SAM–H2804
	SM 92	SAM–H2846

	Station number	*South African Museum number*
Family **Campanulariidae**		
Campanularia hincksii Alder, 1856	SM 23	SAM–H1961
Clytia gravieri (Billard, 1904)	SM 20	SAM–H2859
	SM 79	SAM–H2913
	SM 80	—
	SM 95	SAM–H2926
Clytia paulensis (Vanhöffen, 1910)	SM 16	SAM–H1954
Family **Sertulariidae**		
Sertularella leiocarpa (Allman, 1888)	SM 15	SAM–H1951
	SM 38	SAM–H1979
	SM 86	SAM–H2809
	SM 103	—
*†*Symplectoscyphus amphoriferus* (Allman, 1877)	SM 38	SAM–H1981
	SM 86	SAM–H2810
Symplectoscyphus arboriformis (Markt.-Turn., 1890)	SM 43	SAM–H1980
Symplectoscyphus paulensis Stechow, 1923	SM 100	SAM–H2850
	SM 107	SAM–H2855
*†*Uniscyphus fragilis* g. nov., sp. nov.	SM 43	SAM–H1982
Family **Plumulariidae**		
†*Antennella quadriaurita* Ritchie, 1909	SM 23	SAM–H1962
	SM 38	SAM–H1983
	SM 43	SAM–H1966
	SM 52	SAM–H2877
	SM 83	SAM–H2878
	SM 86	SAM–H2879
	SM 103	SAM–H2880
Cladocarpus distomus Clarke, 1907	SM 67	SAM–H2866
	SM 86	SAM–H2865
	SM 94	SAM–H2864
†*Cladocarpus dofleini* (Stechow, 1911)	SM 86	SAM–H2860
Cladocarpus millardae Vervoort, 1966	SM 86	SAM–H2803
*†*Cladocarpus natalensis* sp. nov.	SM 23	SAM–H1972
	SM 86	SAM–H2861
†*Cladocarpus sinuosus* Vervoort, 1966	SM 23	SAM–H1970
	SM 86	SAM–H2863
	SM 103	SAM–H2862
Halopteris glutinosa (Lamouroux, 1816)	SM 86	SAM–H2869
Halopteris polymorpha (Billard, 1913)	SM 23	SAM–H1959
	SM 86	SAM–H2870
Kirchenpaueria triangulata (Totton, 1930)	SM 52	SAM–H2799
	SM 71	SAM–H2802
	SM 86	SAM–H2863
Nemertesia ramosa Lamouroux, 1816	SM 23	SAM–H1960
	SM 103	SAM–H2853
Plumularia mossambica Millard, 1975	SM 86	SAM–H2867
Thecocarpus flexuosus flexuosus (Lamouroux, 1816)	SM 115	SAM–H2857

SYSTEMATIC ACCOUNT

Family **Bougainvilliidae**

Garveia crassa (Stechow, 1923)

Fig. 1A–C

Bimeria crassa Stechow, 1923*b*: 103. Stechow, 1925: 414, fig. 4.

Description

Colonies growing luxuriantly over the tubes of the polychaet worm, *Loimia* sp., and almost completely obscuring them. Stem strongly fascicled and about 1 mm thick at base, branching freely and quite irregularly, with many of the larger branches reuniting to form a complex meshwork, reaching a maximum height of 40 mm. The thicker parts of the stem commonly containing large spaces between the bundles of tubes, these spaces packed with mud and Foraminifera. Terminal branches unfascicled or lightly fascicled, bearing hydranth pedicels which are usually narrowest at origin and wider distally. Perisarc roughly corrugated and folded throughout, continued over the bases of the hydrothecae to form pseudohydrothecae, but leaving the tentacles free. Hydranth with about nine tentacles.

Gonophores shortly stalked, borne rather sparsely on stem and hydranth pedicels, oval, covered with a thin envelope of perisarc, the largest 0,33 mm long and 0,17 mm wide, in the form of fixed sporosacs, though not mature enough to determine sex.

Nematocysts of at least two kinds:

(i) Desmonemes; 3,6 × 2,4 — 4,2 × 3,2 μm.
(ii) Microbasic euryteles; 5,4 × 2,7 — 6,0 × 3,3 μm.

Remarks

This species was described by Stechow from 741 m off the coast of Somaliland. It is a new record for South Africa, where it occurs in roughly the same depth (720–850 m). Stechow did not mention the substratum and he presumably had only a detached stem available to him. It would be interesting to know whether the species always occurs on polychaet tubes.

In accordance with modern practice the genus *Bimeria* is restricted to those species where the bases of the tentacles are clothed with tubes of perisarc. This species must thus be transferred to the genus *Garveia* Wright, 1859, in which the pseudohydrotheca terminates below the tentacle bases.

Family **Campanulinidae**

Egmundella ?*superba* Stechow, 1921

Fig. 1D–G

Egmundella superba Stechow, 1921: 226. Stechow, 1923*a*: 126, fig. R. Vervoort, 1966: 110, fig. 10.

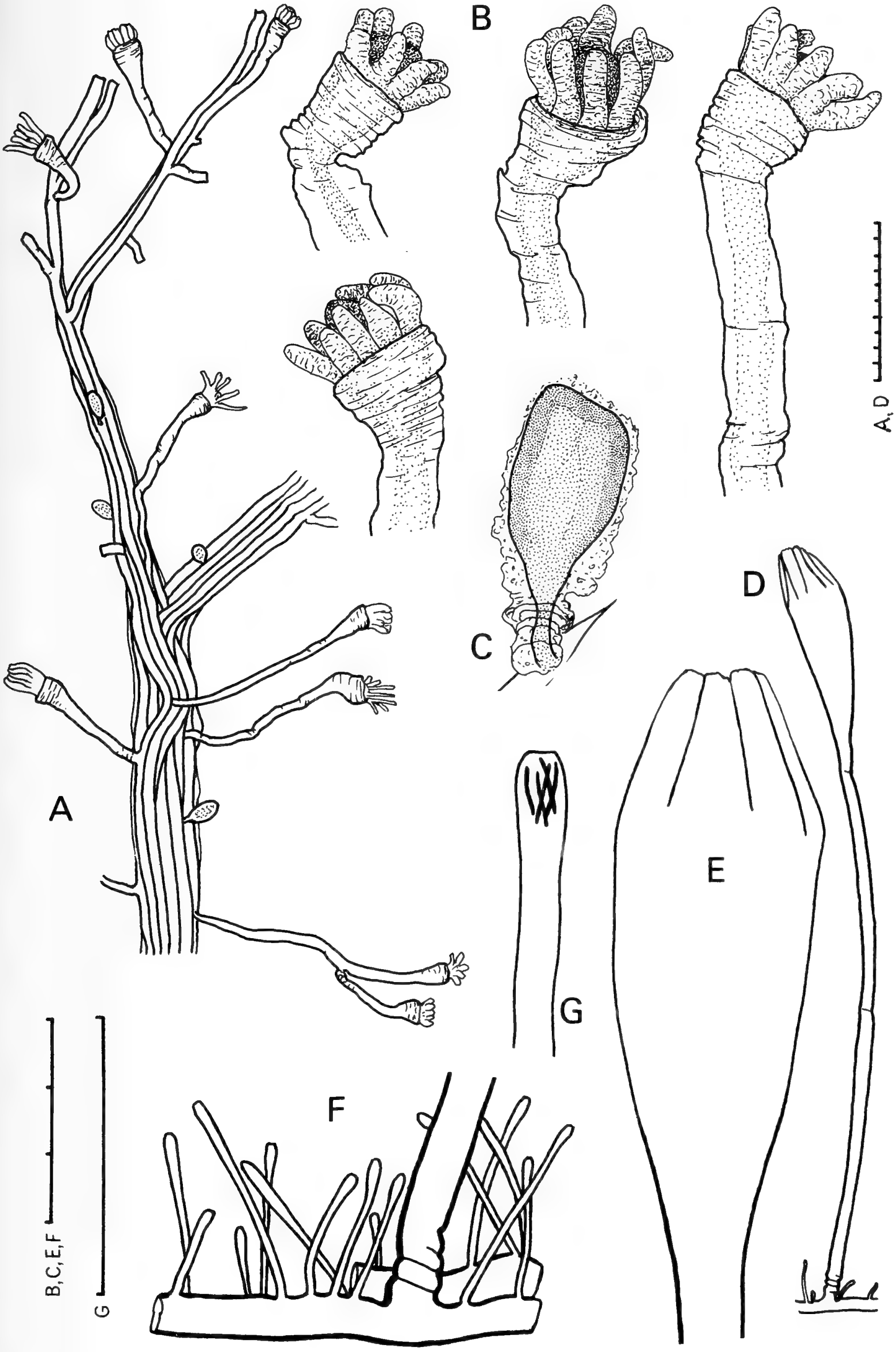

Fig. 1. *Garveia crassa* (Stechow). A. Part of a fascicled stem bearing hydranths. B. Four hydranths. C. Gonophore.

Egmundella ?superba Stechow. D. Hydrotheca and pedicel. E. Hydrotheca. F. Hydrorhiza with nematophores and origin of pedicel. G. Nematophore.

Scale in mm/10.

Description

A colony of seven solitary hydrothecae and many sterile pedicels arising from a hydrorhiza creeping on sponge spicules.

Pedicel long, with two to four distinct annulations close to base, otherwise smooth except for occasional regeneration nodes. Hydrotheca not distinctly demarcated from pedicel, top-shaped and widest at margin, depth two and a half to three and a third times maximum diameter, without diaphragm or annular thickening. Operculum deep, with about eight irregularly folded valves, which are not demarcated from thecal margin. Hydranths completely absent.

Nematothecae abundant, arising from hydrorhiza, of irregular length, tubular but slightly swollen at distal end.

Measurements (mm)

Total length	3,21–6,20
Pedicel, diameter	0,08–0,09
Hydrotheca, approximate depth	0,80–1,20
maximum diameter	0,32–0,38
Nematotheca, length	0,05–0,42
maximum diameter	0,02

Remarks

Of all the known species of *Egmundella* this material most closely resembles *E. superba.* The hydrotheca is slightly broader than that of the holotype (redescribed by Vervoort 1966), but is otherwise similar, and the pedicel is similarly annulated at the base only. The nematothecae differ in their variable length and in their profuse growth which may completely cover the hydrorhiza like a bristly mat.

The type locality and only previous record of *E. superba* is St Thomas, West Indies (depth not given). It is a new record from South Africa.

Opercularella sp.

Fig. 2

Description

Several branched stems reaching 22 mm in height and growing on sponge spicules. Stem branching sympodially, fascicled, giving off alternate hydrothecae from an axial tube, straight or very slightly geniculate, the two rows of hydrothecae in one plane. Branches rather irregular, occasionally subalternate and arising below every third and fourth hydrotheca, similar to stem but unfascicled or lightly fascicled only, the two rows more or less in one plane. Stem and branches either unsegmented or with a faint and very oblique node immediately above the origin of each hydrotheca. Some solitary hydrothecae arising separately from hydrorhiza.

Hydrotheca pedicellate. Pedicel shorter than hydrotheca and not clearly demarcated from it (boundary only recognizable by attachment of hydranth base

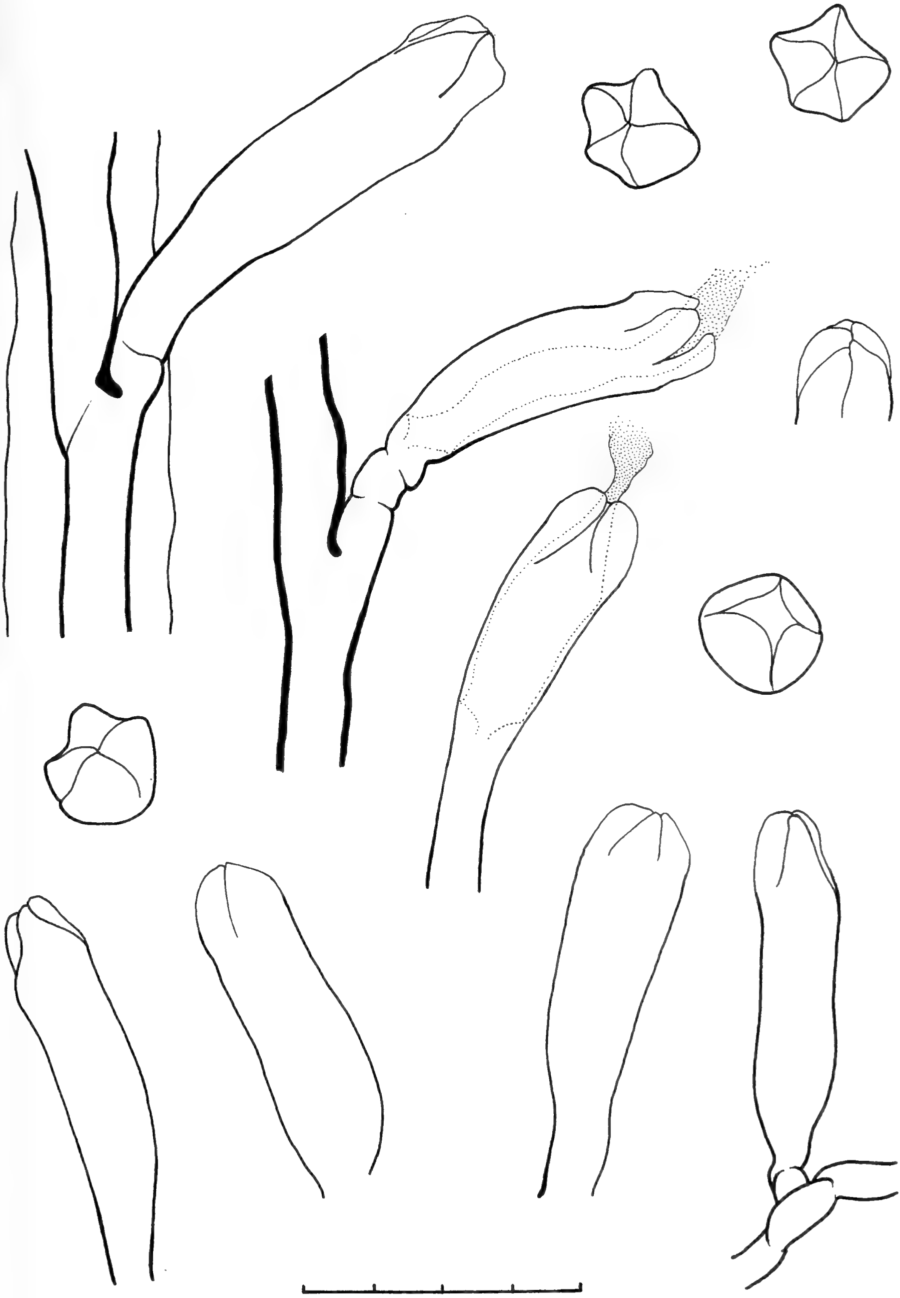

Fig. 2. *Opercularella* sp. Various hydrothecae and opercula, a solitary hydrotheca at bottom right. Scale in mm/10.

to hydrotheca), forming a very acute angle with stem and often pressed against it at base, sometimes with one or two indistinct corrugations. Hydrotheca tubular, asymmetrical and curved away from stem, with adcauline wall more convex than abcauline. Solitary hydrothecae less curved. No diaphragm visible. Operculum of four or five fragile converging segments which are not sharply demarcated from thecal margin.

Gonothecae absent.

Measurements (mm)

Pedicel, length	0,07–0,26
Hydrotheca, length abcauline . .	0,35–0,54
maximum diameter	0,11–0,16

Remarks

This material is unlike any other described species. It is perhaps closest to '?*Opercularella* spec. no. 2' of Vervoort (1966: 108), but differs from it in the curved hydrothecae and the smaller number of opercular segments. The operculum is very delicate and crumples easily; it can only be seen clearly by slicing off the top of the hydrotheca and viewing from above. Since the material is not very well preserved and is infertile the writer prefers not to describe it as a new species.

Stegolaria geniculata (Allman, 1888)

Fig. 3

Cryptolaria geniculata Allman, 1888: 41, pl. 20 (figs 1, 1*a*, 1*b*).
?*Cryptolaria operculata* Nutting, 1905: 947, pl. 3 (fig. 4), pl. 10 (figs 12–14). Ritchie, 1910: 9.
Stegopoma operculatum: Billard, 1941: 16, fig. 1.
Stegolaria geniculata: Vervoort, 1946: 299, figs 2–3. Edwards, 1973: 593.
Stegolaria operculata: Edwards, 1973: 594.

Description

Several branching fan-shaped stems reaching a maximum height of 40 mm and several smaller ones, growing on a gorgonian skeleton, sponge spicules and a worm tube.

Stem strongly fascicled, giving rise to alternate hydrothecae and roughly alternate or subalternate branches from an axial tube. Branches similar to stem, fascicled almost to the end. The two rows of branches and hydrothecae in one plane.

Hydrotheca tubular, curved smoothly outwards, adnate to stem or branch for half to two-thirds height and in the thicker parts of the stem with the adnate part immersed among the peripheral tubes. Axillary hydrotheca with abcauline wall adnate to branch. Base of hydrotheca without diaphragm or perisarcal thickening, but usually demarcated by an indentation of the abcauline wall. Distal part of hydrotheca very delicate and usually damaged. Operculum of the *Stegopoma* type, consisting of two pleated valves seated in the embayments between two gable-like processes of the margin.

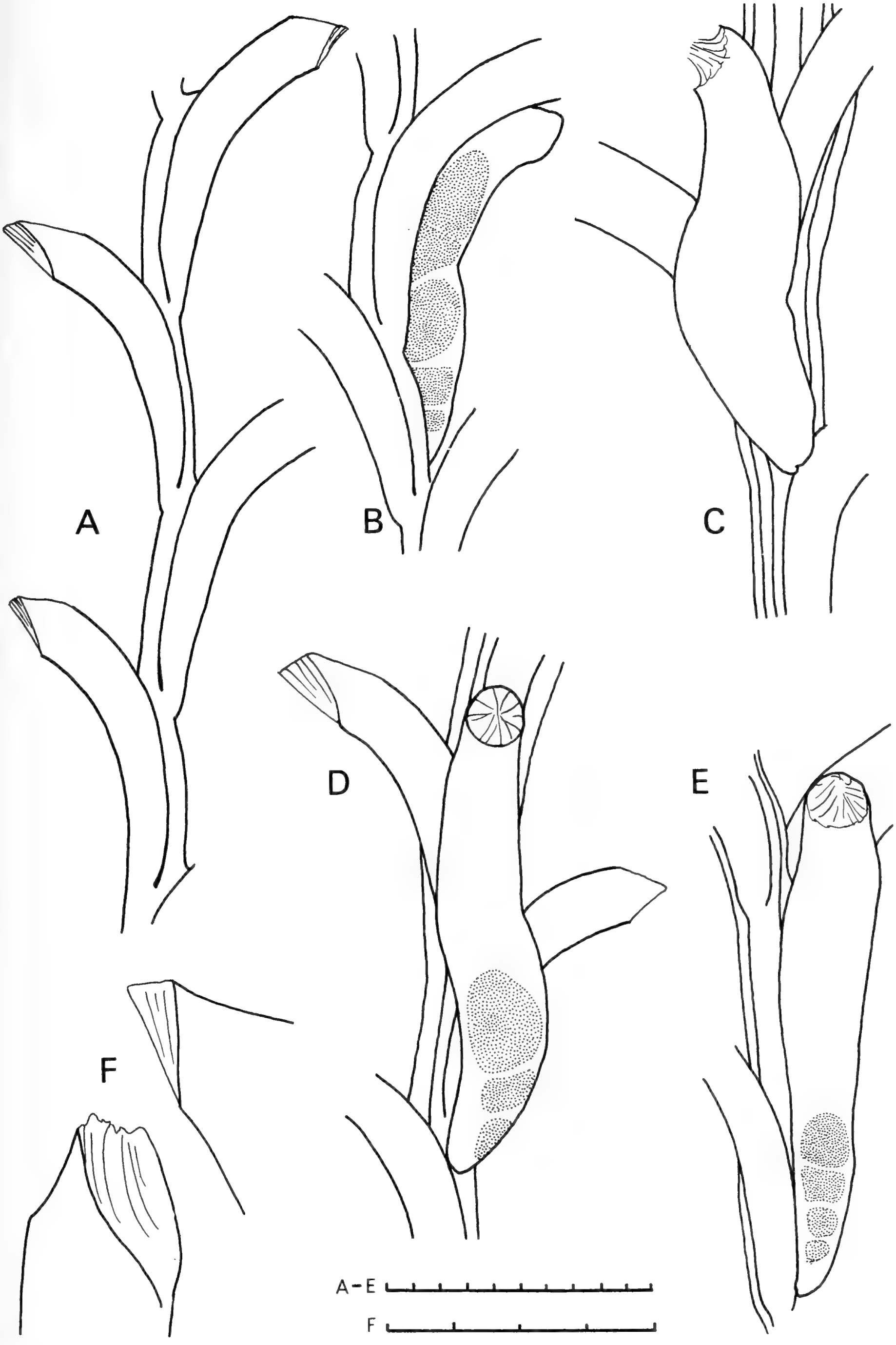

Fig. 3. *Stegolaria geniculata* (Allman). A. Part of stem from distal end. B–E. Parts of stem with gonothecae. F. Distal ends of two hydrothecae to show opercula. Scale in mm/10.

Gonotheca sac-shaped, completely adnate to branch. Aperture facing away from branch and sometimes raised slightly above it, subterminal, circular, with an operculum of fragile converging segments. Containing up to five gonophores (probably male) one above the other.

Measurements (mm)

Hydrotheca, length abcauline (approx.)	0,96–1,62
length adcauline, adnate part	0,72–0,96
length adcauline, free part	0,36–0,93
diameter at mouth	0,19–0,40
Gonotheca, length	1,11–2,02
maximum diameter	0,26–0,46
diameter of aperture	0,17–0,23

Remarks

The author can see little to distinguish *Stegolaria operculata* from *S. geniculata* other than the markedly geniculate stem of the latter. In the present material the degree of geniculation is variable and in general intermediate between the two, the tips of some branches being almost as geniculate as those illustrated by Allman and Vervoort for *S. geniculata* and other branches being completely straight as in *S. operculata*. She has therefore united the two species. The gonothecae are exactly like those described by Vervoort (1946).

The genus *Stegolaria* has been retained in view of the peculiar gonothecae; since these contain fixed sporosacs the genus cannot be united with *Modeeria*. The status of *Stegopoma* awaits further information on reproduction.

Distribution

Fiji (type locality), Hawaii, East Indies (Celebes and Kei Island), Malay Archipelago. A deep-water species ranging from 253 to 910 m. A new record from South Africa.

Family **Lafoeidae**

Lafoea dumosa (Fleming, 1820)

Remarks

The opinion of Cornelius (1975) is accepted that *Lafoea fruticosa* (M. Sars) is a synonym for *L. dumosa* (Fleming). This cosmopolitan species is well known from deeper waters of the South African coast.

Zygophylax brownei Billard, 1924

Fig. 4

Lafoea pinnata: Browne, 1907: 25.
Zygophylax pinnata: Billard, 1923: 14, fig. 1A.
Zygophylax brownei Billard, 1924: 64. Leloup, 1940: 11, pl. 1 (fig. 7). Patriti, 1970: 28, fig. 30.

Description

Two colonies with stems reaching a maximum height of 61 mm, stiff, fascicled, bearing alternate hydrothecae and subalternate branches in one plane. Branches usually arising immediately below every third and fourth hydrotheca, bearing alternate hydrothecae, sometimes rebranching in a similar manner to the stem. Where the branching follows this regular subalternate scheme, both hydrothecae and branches arise from a single axial tube, but this arrangement is sometimes obscured by extra branches and hydrothecae from peripheral tubes. These possibly represent auto-epizootic colonies but it is no longer possible to distinguish the hydrorhizae.

Hydrotheca and pedicel together forming a bilaterally symmetrical tubular figure which is more convex on the adcauline side. Pedicel with no node separating it from the apophysis but demarcated by an indentation on adcauline side, separated internally from hydrotheca by a well-developed diaphragm. Hydrotheca everted at margin.

Nematothecae scarce, occurring singly on stem apophyses, usually only one or two to a stem; tubular, with everted margin, variable in length.

Gonothecae (present in Station SM 23) quite separate from one another, not conjoined in a coppinia but clustered thickly round certain parts of the stem; deep-oval, not compressed, with two apertures (rarely three), each on the end of a recurved tubular neck; containing planula larvae; with no special accumulations of nematothecae.

Measurements (mm)	*Station SM 23*	*Station SM 86*
Pedicel, length adcauline	0,06–0,10	0,05–0,12
Hydrotheca, length adcauline	0,34–0,41	0,31–0,47
diameter at margin	0,16–0,19	0,14–0,18
Gonotheca, length	0,08–1,32	—
maximum diameter (below necks)	0,31–0,38	

Remarks

Z. brownei is closely related to *Z. biarmata* Billard, 1905, and is in fact included with it by Broch (1918). It is, however, retained as a separate species by Leloup (1940) on the basis of the sparser distribution of nematothecae. This is the first record of *Z. brownei* from the southern hemisphere and the first description of gonothecae; the latter are similar in general shape to those of *Z. biarmata* (as described by Saemundsson (1912) under the name of *Lictorella levinseni*) but are proportionally longer and more slender, and are without the numerous nematothecae described by Broch (1918).

Both these species have a north Atlantic distribution. Records of *Z. biarmata* from other parts of the world (Jäderholm 1919, from Japan; Jarvis 1922, from east Africa) were all sterile and thus still need confirmation.

Distribution

Eastern North Atlantic from France to Morocco, 20–752 m. Type locality: Bay of Biscay. A new record from South Africa.

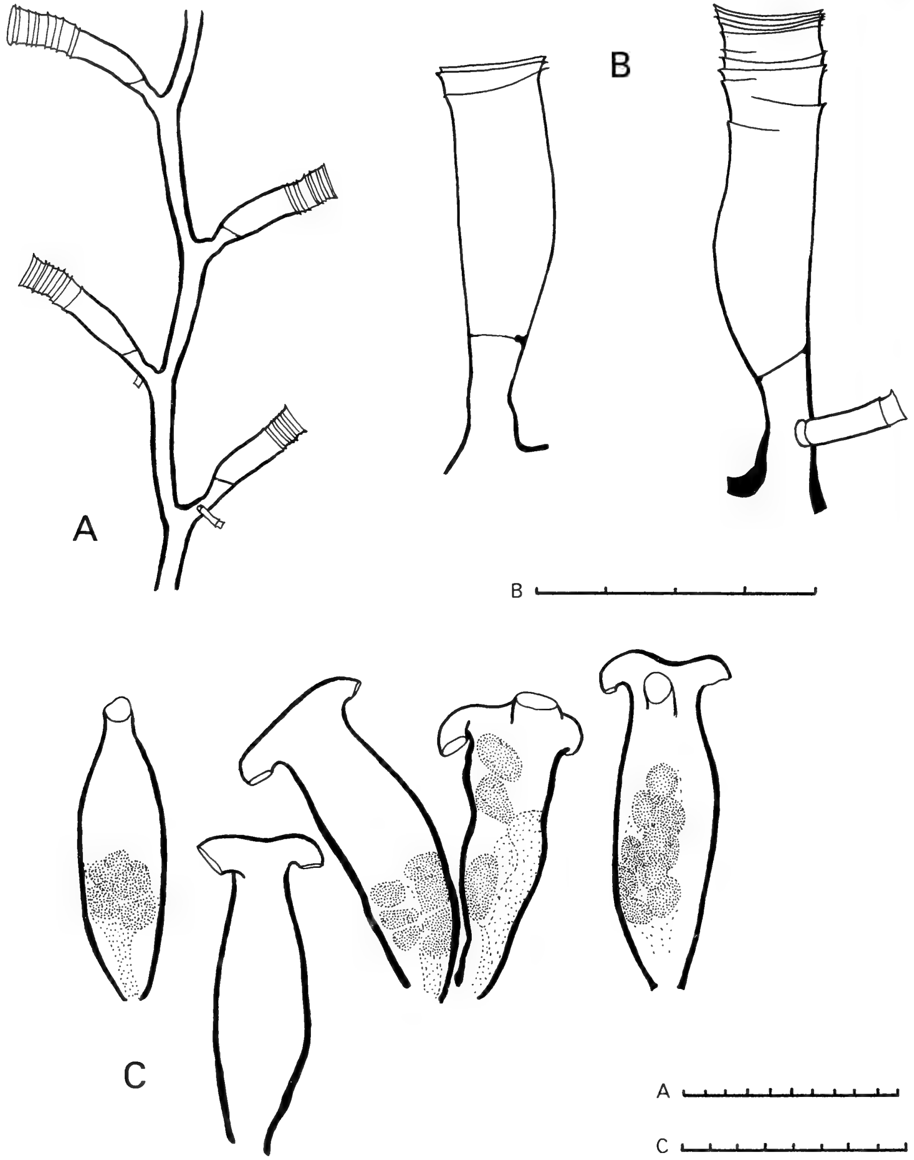

Fig. 4. *Zygophylax brownei* Billard. A. Part of stem. B. Hydrothecae. C. Gonothecae, that on extreme left in side view, the two on extreme right each with three openings. Scale in mm/10.

Zygophylax inconstans sp. nov.

Fig. 5

Material

Holotype: SAM–H1975. Station SM 23: 27°44,4'S 32°42,8'E, 400–450 m.
Other material: SAM–H1977. Station SM 43: 28°45,5'S 32°24,5'E, 360–420 m.

Description of holotype

Colony growing on a polyzoan and consisting of slender, straggling stems often reattaching to one another and to the polyzoan and producing a tangled irregular growth one or two centimetres in height. Stem unfascicled or lightly fascicled, unbranched or branching irregularly and in any plane, unsegmented, geniculate, bearing alternate hydrothecae on short apophyses which arise at the 'elbows'. Peripheral tubes arising at origins of branches.

Hydrotheca and pedicel not sharply demarcated externally, together forming a deep-campanulate figure which may be radially symmetrical or slightly bilaterally symmetrical with the adcauline surface more convex than the abcauline. Margin of hydrotheca everted. Diaphragm distinct, usually oblique.

Nematothecae numerous, one to three on each apophysis (usually two), and scattered on peripheral tubes of stem and on hydrorhiza; tubular, two-chambered, with short basal chamber and long distal chamber, with everted margin.

Coppiniae present surrounding thicker parts of stem, consisting of a mass of conjoined gonothecae, but without modified hydrothecae or nematothecae. Gonotheca saccular and of irregular shape, with a single aperture with a flared margin on the summit of a short tubular neck.

Measurements (mm)

Pedicel, length adcauline		0,03–0,06
Hydrotheca, length adcauline		0,22–0,30
diameter at margin		0,10–0,12
Gonotheca, length	reaching	0,72
maximum diameter	reaching	0,52

Remarks

The ramifications of these colonies are so intimately associated with the polyzoan that it is almost impossible to separate the two. The hydrorhiza runs along the upright stem of the host, separating from it and attaching to other parts at intervals; it produces erect stems, solitary hydrothecae and numerous nematothecae.

There are two species of *Zygophylax* which share certain characters with this material, namely a closed coppinia, a gonotheca with a single terminal aperture, small deep-campanulate hydrothecae, and two nematothecae to each hydrotheca-bearing apophysis. These are *Z. armata* (Ritchie, 1907) and *Z. profunda* Quelch,

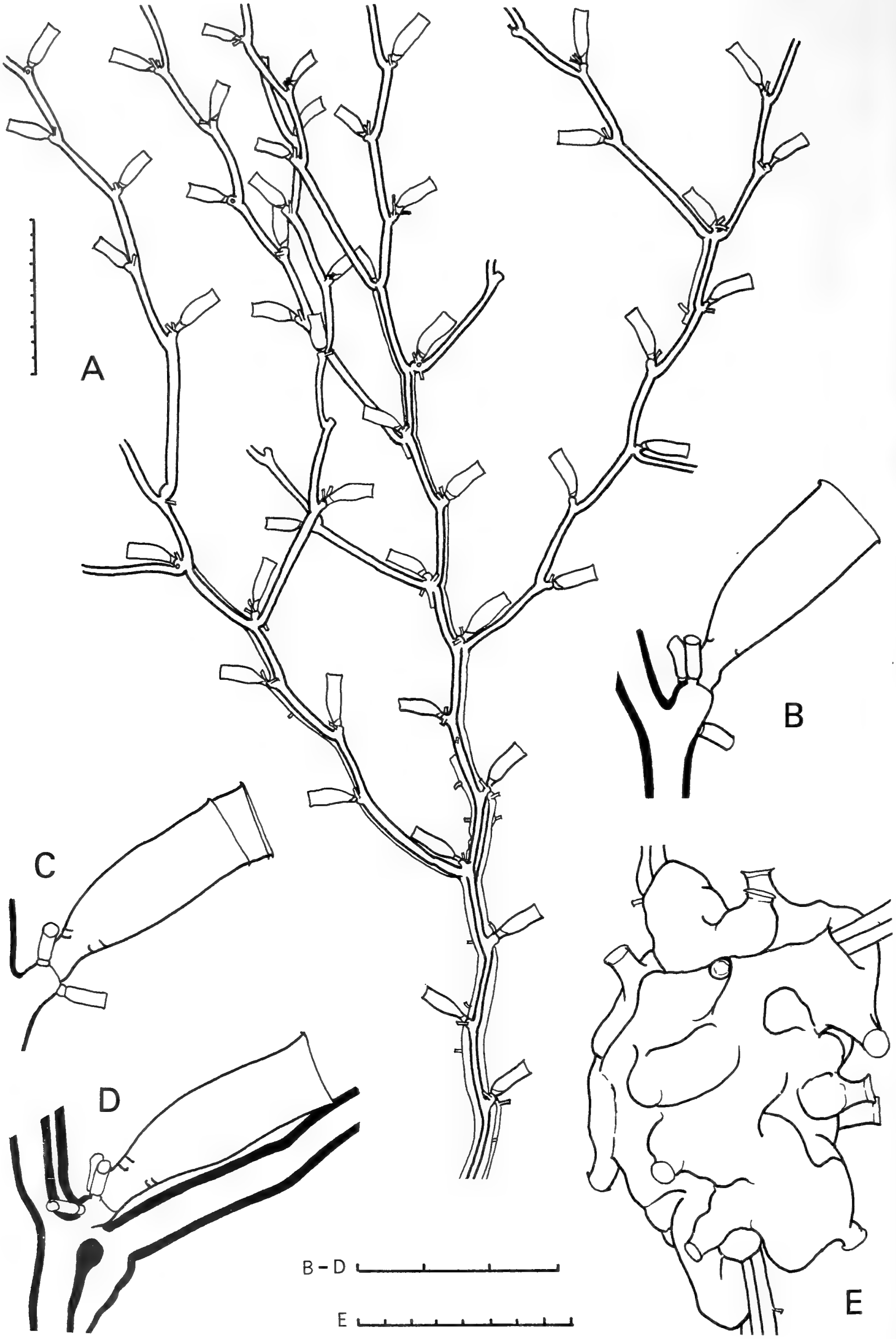

Fig. 5. *Zygophylax inconstans* sp. nov. from the holotype, SAM–H1975. A. Part of stem. B–C. Hydrothecae. D. Axillary hydrotheca, and origin of peripheral tubes. E. Coppinia. Scale in mm/10.

1885. Both of these have a much stiffer colony and a more heavily fascicled stem, and in both the coppinia is provided with numerous long branching nematothecae. In *Z. armata* the gonothecae are more regular and hexagonal in section. The schizoholotype of *Z. profunda* from Cape Verde is a mounted slide (B.M. no. 85.7.21.1) of infertile fragments in very poor condition. The hydrothecae are shorter and more strongly curved than in the present material (Fig. 6A). The fertile material from Madeira assigned to *Z. profunda* by Totton (1930) (slide B.M. no. 19.8.15.2) has hydrothecae more similar in shape to the present material though very slightly smaller (Fig. 6B–C). The coppinia is identical apart from the presence of branching nematothecae. It is mainly this last character that thus separates *Z. profunda* from *Z. inconstans*.

Family **Sertulariidae**

Symplectoscyphus amphoriferus (Allman, 1877)

Fig. 7A–D

Sertularella amphorifera Allman, 1877: 22, pl. 15 (figs 8–10). Nutting, 1904: 88, pl. 20 (figs 1–2). Billard, 1906: 183.
Symplectoscyphus ?amphoriferus: Millard, 1967: 182, fig. 4E–F.

Description

Several unfascicled stems reaching a maximum height of 21 mm, some of them branching alternately. Stem and branches geniculate in distal parts. Branches given off at a wide angle (over 80°) and with a dichotomous effect due to a more strongly marked geniculation at the origin of each branch. Nodes indistinct.

Hydrotheca deep and slender, adnate for about one-third adcauline length, curved outwards, adcauline free part straight or slightly concave. Margin with three teeth, one adcauline and two latero-abcauline. No internal teeth.

One gonotheca present, pear-shaped, with eleven raised transverse ridges and a slender terminal neck.

Measurements (mm)

Internode length	0,60–0,98
Hydrotheca, length abcauline	0,36–0,43
length adcauline, adnate part	0,20–0,23
length adcauline, free part	0,33–0,40
diameter at margin	0,12–0,14
Gonotheca, length	1,22
maximum diameter	0,74

Remarks

This material is very similar to that recorded from the southern Indian Ocean (Millard 1967). The presence of pseudodichotomous branches and a larger pro-

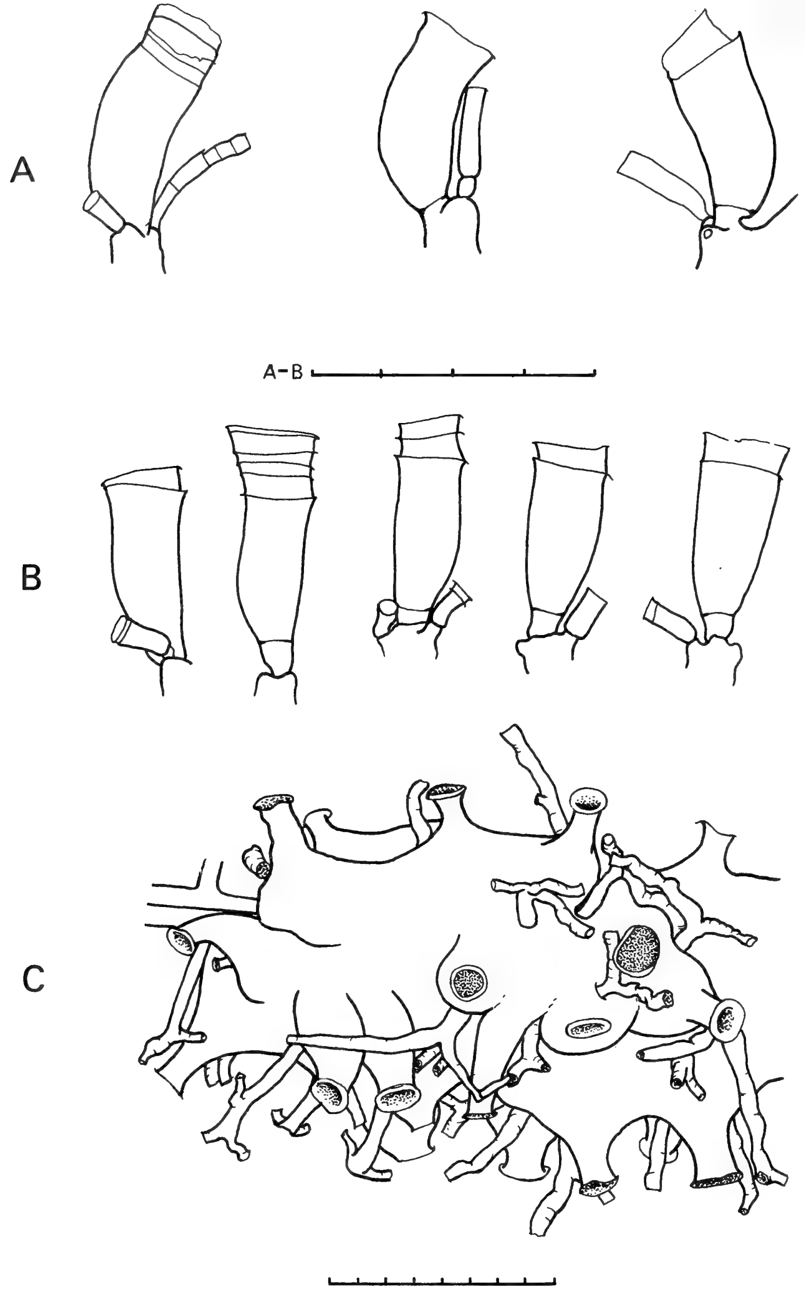

Fig. 6. *Zygophylax profunda* Quelch. A. Hydrothecae from the schizoholotype, BM 85.7.21.1. B. Hydrothecae, and C, coppinia, from Totton's material, BM 19.8.15.2. Scale in mm/10.

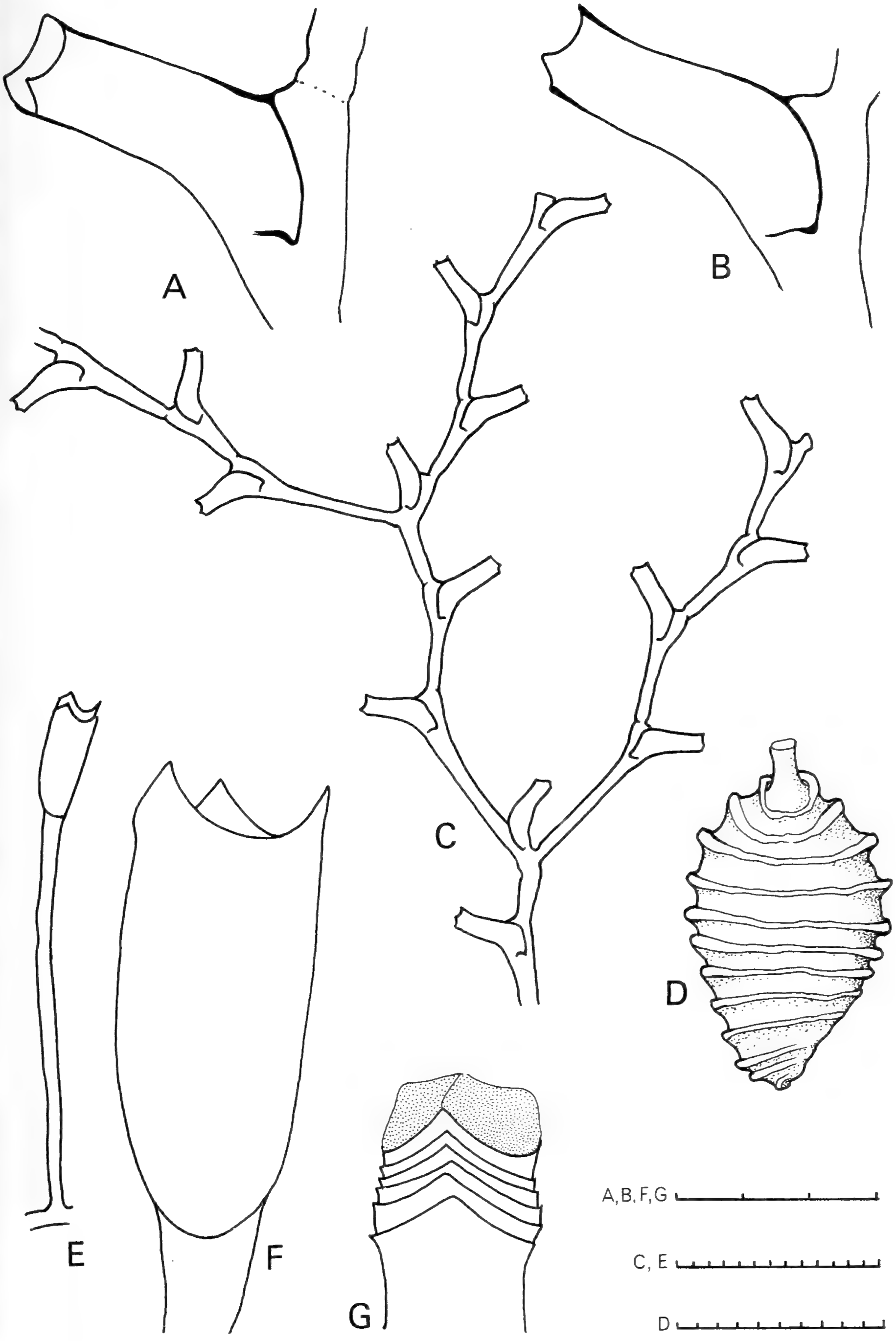

Fig. 7. *Symplectoscyphus amphoriferus* (Allman). A–B. Hydrothecae. C. Part of stem. D. Gonotheca.

Uniscyphus fragilis sp. nov. from the holotype, SAM–H1982. E. Hydrotheca and pedicel. F. Hydrotheca. G. Distal end of hydrotheca with regenerated margins and operculum.

Scale in mm/10.

portion of the hydrotheca adnate to the stem is closer to the type material and supports the identification.

Distribution

Except for one record from the southern Indian Ocean, this species is known only from the northern Atlantic from the West Indies to south-east of Iceland. All the records are from deep water and range from 185 to 1 256 m. Type locality: Double-headed Shot Key. A new record from South Africa.

Uniscyphus gen. nov.

Diagnosis

Colony stolonial, with pedicellate hydrothecae arising direct from a creeping hydrorhiza. Hydrotheca cylindrical, with three marginal teeth and an operculum of three valves seated in the bays between the teeth and meeting in the centre as a pyramid.

Type species: *Uniscyphus fragilis* sp. nov.

Uniscyphus fragilis sp. nov.

Fig. 7E–G

Material

Holotype: SAM–H1982. Station SM 43: 28°45,5′S 32°24,5′E, 360–420 m. Five hydrothecae, three mounted on a slide.

Description

Hydrorhiza creeping. Hydrotheca solitary, pedicellate. Pedicel long, at least three times length of hydrotheca, slender, not annulated, arising at right angles to hydrorhiza. Hydrotheca terminal, cylindrical, not annulated, with three well-developed, equally spaced marginal teeth. No internal teeth. Operculum of three valves. Gonothecae absent.

Measurements (mm)

Pedicel length	2,4–3,9
Hydrotheca, depth to tips of teeth	0,70–0,75
diameter at margin	0,25–0,29
diameter/depth	0,34–0,41

Remarks

There is no existing genus to contain this delicate species. In its stolonial form it resembles *Calamphora*, which, however, has four marginal teeth and an annulated hydrotheca. It seems to bear the same relationship to *Parascyphus* that *Calamphora* bears to *Sertularella*. The hydranths are not well preserved, and, although it is difficult to be certain, no abcauline blind pouch could be seen.

Family **Plumulariidae**

Antennella quadriaurita Ritchie, 1909

Fig. 8

Antenella quadriaurita Ritchie, 1909: 92, fig. 9. Leloup, 1932: 162, pl. 16 (fig. 2).
Antennella quadriaurita: Stechow, 1919: 113. Millard, 1966: 492.
Antenella quadriaurita, forma *africana* Broch, 1914: 26.
Antenella africana: Stechow, 1925: 492, fig. 11.
Antennella africana: Millard, 1975: 331, fig. 107A–E.

Discussion

The seven samples of *Antennella*, of which only the last two were fertile, have long, slender athecate internodes bearing two to four nematothecae each. This suggested an affinity with *A. quadriaurita* rather than with the South African species *A. africana* (both are species with two pairs of lateral nematothecae), and since there was already a doubt as to the separate entity of these two species a reappraisal of the South African material was undertaken. Also available for comparison was a new sample from Tristan da Cunha (SAM–H1949), and another from Nightingale Island (SAM–H1991), both collected in 1971.

It has previously been claimed (Millard 1975) that the only character separating these two species is the presence of, usually, one nematotheca on each athecate internode in *A. africana* and two or three in *A. quadriaurita*. Counts of nematothecae in the available samples (Table 1) show no geographical relationship. For example, the sample from Tristan has one nematotheca on 82 per cent of the internodes, as against Ritchie's type of *A. quadriaurita* from Gough Island, and material from the Vema Seamount (South Atlantic), where most internodes have two or three nematothecae. On the west and south coasts of South Africa most internodes have one nematotheca, yet in the sample from Port Elizabeth all internodes have two nematothecae, and in the seven samples of the present collection from Natal most have two or three.

There does, however, appear to be a relationship between the number of nematothecae and the length of the internode. This is demonstrated in Figure 8, whence it is apparent that, although there is much variation within a sample, in general longer internodes have more nematothecae. This diagram also indicates that the seven deep-water samples from Natal (Numbers 14–15, 17–21) are most closely related to the type material from Gough Island (Number 16), from which they are most distant geographically.

Within a single colony, the longer athecate internodes bearing several nematothecae tend to occur near the base of a hydrocladium and shorter ones with one nematotheca near the distal end.

From these considerations it is concluded that *A. quadriaurita* and *A. africana* cannot be retained as separate species, and the latter is sunk in the former.

The distribution of the composite species is:

Central and South Atlantic Ocean, including Havanna (Stechow 1919), the Tristan da Cunha group (Ritchie 1909, and this work), tropical west Africa

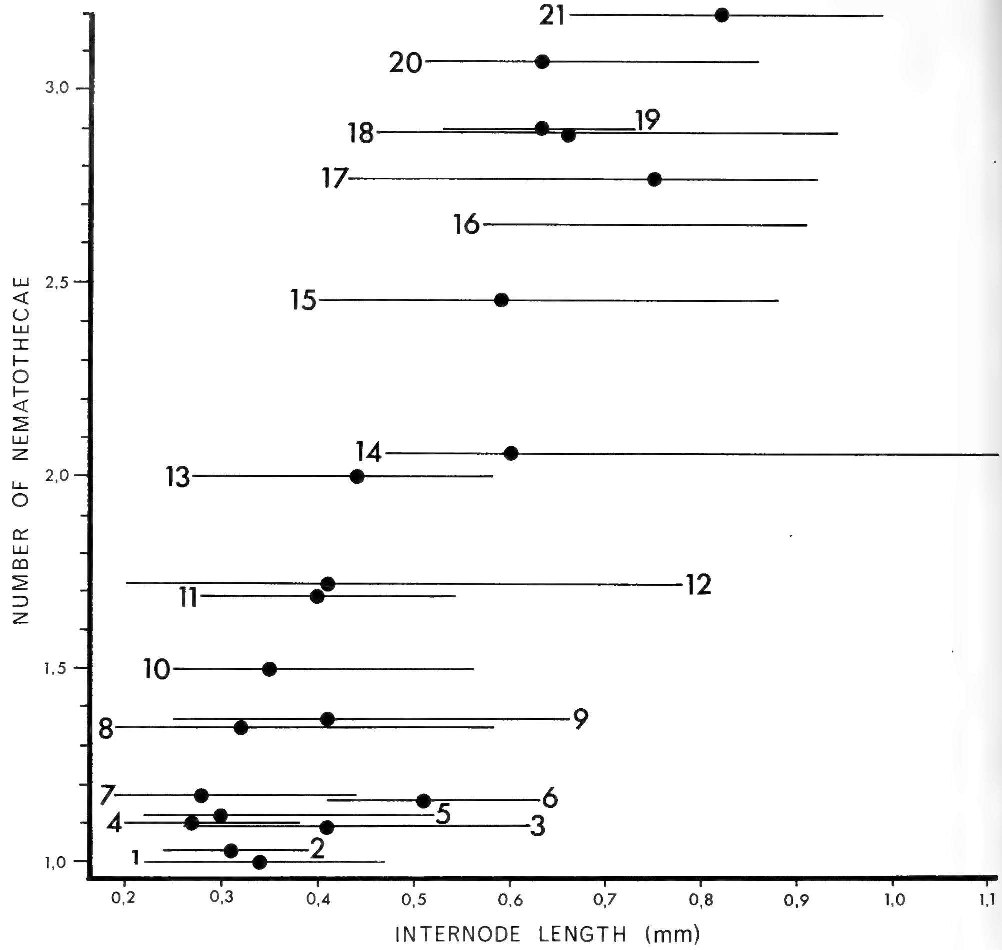

Fig. 8. The average length, with range, of the intermediate athecate internodes related to the number of nematothecae which they bear in different samples of *Antennella*.

1. False Bay
2. Table Bay
3. Agulhas Bank (34°30′S 20°56′E)
4. West of Cape Peninsula
5. Lambert's Bay
6. Agulhas Bank (34°35′S 21°23′E)
7. Mossel Bay
8. Nightingale Island
9. Saldanha Bay
10. Off Lüderitz Bay
11. Vema Seamount
12. Tristan da Cunha
13. Port Elizabeth
14. Off Natal (SM 43)
15. Off Natal (SM 23)
16. Gough Island (from Ritchie 1909)
17. Off Natal (SM 86)
18. Off Natal (SM 83)
19. Off Natal (SM 103)
20. Off Natal (SM 38)
21. Off Natal (SM 52)

(Broch 1914), Vema Seamount (Millard 1966), and South Africa (Millard 1975);

Indian Ocean, including India (Leloup 1932) and South Africa (Millard 1975);

Pacific Ocean, including New Zealand (Ralph 1961).

The type locality is Gough Island (Ritchie 1909).

TABLE 1

The percentage number of nematothecae per athecate internode for various samples of *Antennella*. The samples are arranged geographically, starting with the Atlantic stations and west coast, and ending with the Natal coast. The last seven samples are those from this collection.

	Number of nematothecae per internode, per cent				*n*	*Depth (m)*
	1	2	3	4		
Gough Is. (from Ritchie 1909)	—	40	55	5	20	183
Tristan	82	16	2	—	308	?
Nightingale Is.	80	20	—	—	35	?
Vema Seamount	23	74	2	—	90	42–50
Lüderitz Bay	69	30	1	—	226	35
Lambert's Bay	92	8	—	—	101	20
Saldanha Bay	74	25	1	—	118	35
Table Bay	98	2	—	—	53	9
West of Cape Peninsula	95	5	—	—	19	79
False Bay	99	1	—	—	311	0–27
Agulhas Bank: 34°30′S 20°56′E	89	11	—	—	28	73
Agulhas Bank: 34°35′S 21°23′E	80	20	—	—	30	68
Mossel Bay	63	37	—	—	38	10–20
Port Elizabeth	—	100	—	—	31	9
Natal, SM 43	2	95	3	—	113	360–420
Natal, SM 103	—	22	67	11	9	680
Natal, SM 38	—	29	64	7	14	775–825
Natal, SM 83	—	11	89	—	28	600–810
Natal, SM 86	—	23	77	—	48	550
Natal, SM 23	—	51	47	2	100	400–450
Natal, SM 52	—	—	80	20	15	720

Cladocarpus dofleini (Stechow, 1911)

Fig. 9D–F

Dinotheca dofleini: Stechow, 1925: 508, figs 49–52. Vervoort, 1966: 162, figs 63–64.
Cladocarpus dofleini: Millard, 1975: 421, fig. 130G.

Description

Two fascicled stems bearing phylactocarps, the longer 90 mm in height. Structure and dimensions very similar to those of Vervoort (1966), to which the following points may be added.

The number of cauline nematothecae between two successive hydrocladia varies from two in the distal region of the stem to six in the proximal part. The hydrocladial internodes have a shorter distal region than those illustrated by

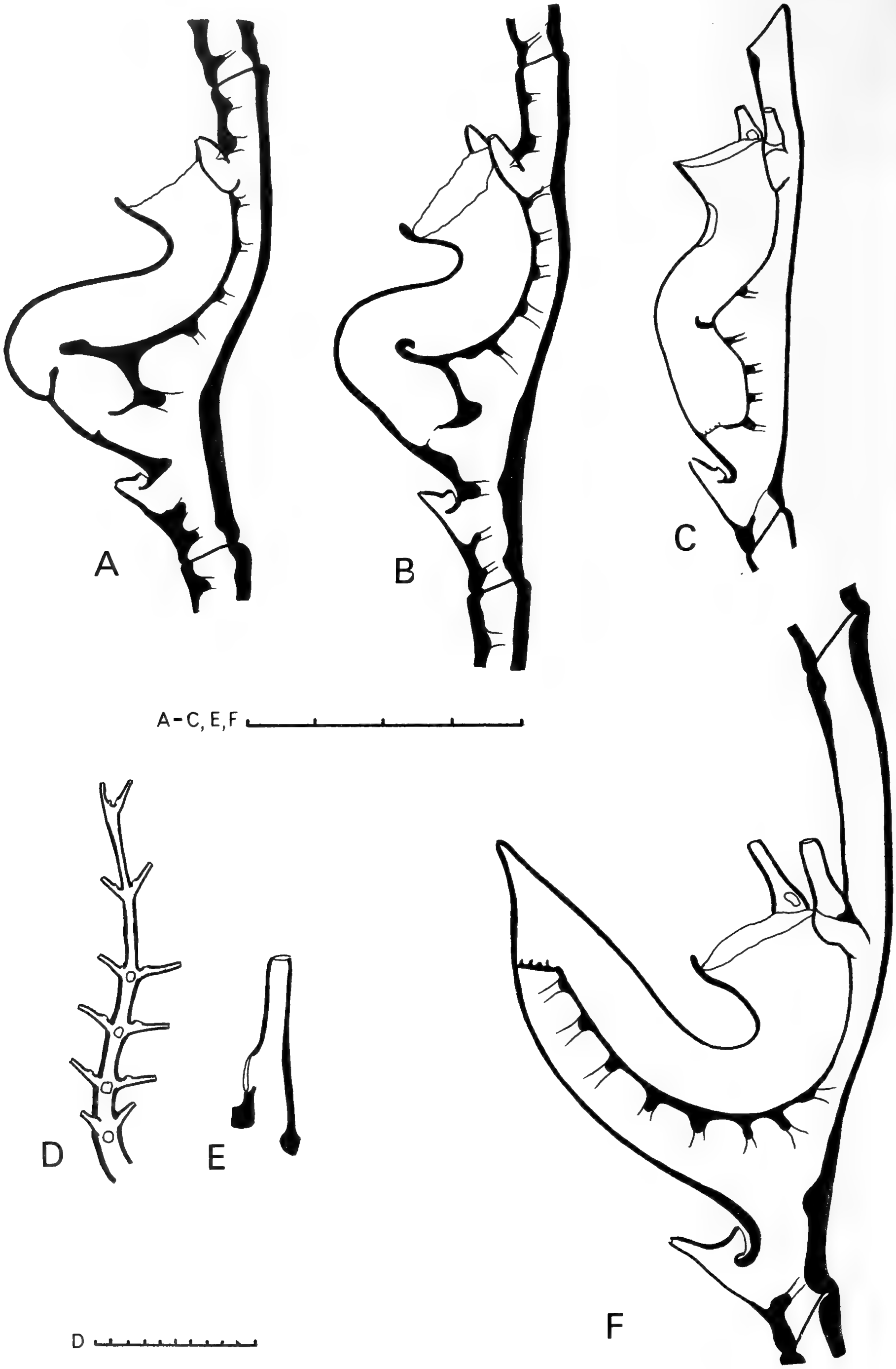

Fig. 9. *Cladocarpus sinuosus* Vervoort. A. Hydrotheca with an abcauline intrathecal septum, and B, one without. C. Hydrotheca of var. *edentatus* Vervoort.

Cladocarpus dofleini (Stechow). D. Phylactocarp, and E, one of its nematothecae. F. Hydrotheca.

Scale in mm/10.

Stechow (1925) and are more like those of Vervoort, but the 'spine' on the hydrotheca is long, like that of Stechow. The distal end of the internode is occasionally cut off as a short athecate internode. The phylactocarps are similar to those described by Stechow, but have no gonothecae.

Measurements (mm)

Hydrocladium, internode length	0,87–0,98
Hydrotheca, distance from adcauline edge to spine	0,42–0,55
diameter at margin	0,20–0,27

Remarks

This rare species is known from the African coast from the equator to the Agulhas Bank, and occurs only in depths over 425 m.

Cladocarpus natalensis sp. nov.

Fig. 10

Material

Holotype: SAM–H2861. Station SM 86: 27°59,5′S 32°40,8′E, 550 m. Five stems, fertile.

Other material: SAM–H1972. Station SM 23: 27°44,4′S 32°42,8′E, 400–40 m.5 Five stems, infertile.

Description of holotype

The tallest stem 50 mm in height and bearing about seventy alternate hydrocladia. Hydrorhiza mat-like. Stem fascicled, unbranched, bearing the hydrocladia from an axial tube which is exposed on the anterior surface. Two cauline nematothecae between the origins of any two consecutive hydrocladia, of which one is axillary. Five or six septa present between two consecutive hydrocladia in the older part of the stem, but septa absent in the distal part. Segmentation obscure.

Hydrocladia 4–6 mm in length and bearing up to ten hydrothecae on anterior surface, consisting of sigmoidally curved thecate internodes separated by straight or slightly oblique nodes. Each internode with numerous septa (12–16), one hydrotheca and three nematothecae (one median inferior and one pair laterals). Distal part of internode short and terminating just above thecal margin.

Hydrotheca sigmoidally curved; abcauline wall very strongly convex immediately above base, strongly concave above this and with the maximum concavity at about half height, then widening to margin; base carried forwards with curvature and taking with it the adthecal ends of three or four internodal septa; the basal convexity capped by a hollow perisarcal horn of variable length and direction; adcauline wall strongly curved near base, the curvature decreasing smoothly to margin. A curved adcauline intrathecal septum present in basal region and close above thecal floor. Margin with one inturned median abcauline tooth, with the rest of the edge irregularly serrated and often lower at the adcauline side, forming an angle of 50–80° with the distal end of the internode.

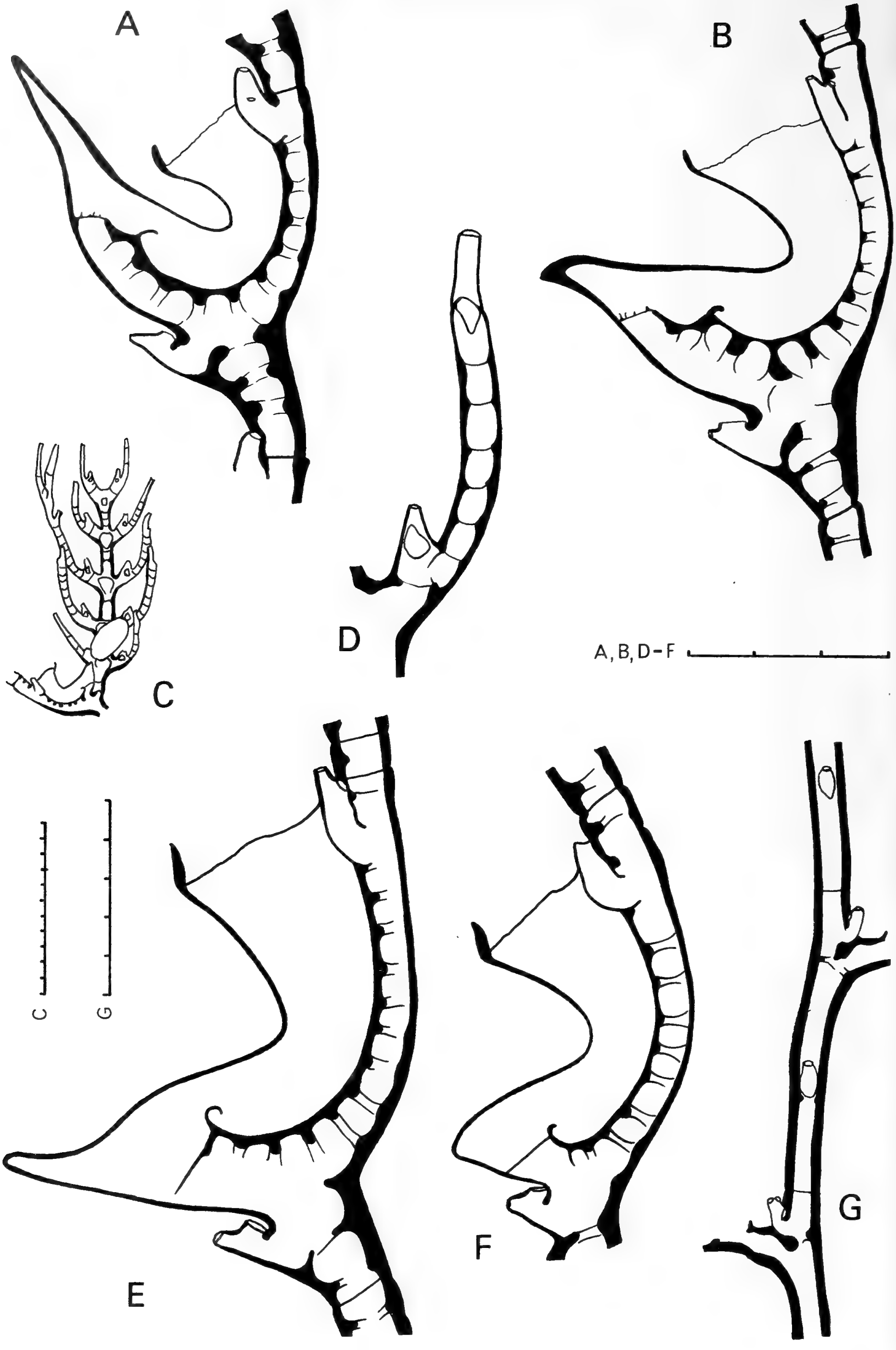

Fig. 10. *Cladocarpus natalensis* sp. nov. A–D from the holotype, SAM–H2861, and E–G from SAM–H1972. A–B. Hydrothecae. C. Phylactocarp, and D, one of its nematothecae. E–F. Hydrothecae. G. Part of stem showing cauline nematothecae and origins of two hydrocladia. Scale in mm/10.

Median inferior nematotheca free from hydrotheca and seated well below its base, with two apertures, one terminal and one on upper surface near base. Lateral nematotheca overtopping thecal margin, bifurcated, with two terminal apertures, one more elevated than the other, and one on mesial surface.

Phylactocarps borne one on first internode of hydrocladium and rarely one on second internode as well, curved forwards and forming a double row on front of stem. Phylactocarp bearing a double row of long nematothecae, with many septa both in the nematothecae and in the main axis. Nematotheca with four apertures, one terminal, one subterminal, one on the end of a tubular process near base, and one on the side of this tubular process. Gonothecae absent except for one empty one; this is oval and with a terminal aperture.

Measurements (mm)	*Holotype* *SAM–H2861*	*SAM–H1972*
Hydrocladium internode length	0,51–0,74	0,80–0,96
Hydrotheca, depth, abcauline base to tip of median tooth	0,18–0,35	0,29–0,58
depth, horn to adcauline edge	0,34–0,52	0,43–0,75
diameter at margin	0,17–0,21	0,23–0,29

Variation and remarks

In this species the degree of curvature of the hydrotheca and the length of the horn vary markedly from stem to stem, and to a certain degree within the same stem. In SAM–H1972 the horn may vary from hardly recognizable (as in *C. inflatus* Vervoort) to about twice the width of the base, and is usually directed obliquely downwards. In the holotype the horn is in general longer and the hydrotheca more curved, so that in extreme cases the horn points obliquely upwards parallel with the axis of the distal half of the hydrotheca and reaching well beyond the distal end of the internode. The extreme variations in the two samples are illustrated in Figure 10.

Other variations include one branching hydrocladium which has developed as a stem, a branching nematotheca on the phylactocarp (Fig. 10C), and the presence of minute teeth round the edge of the hydropore in some hydrothecae. The internodal septa may be as many as 20 in the second sample.

In the curvature of the hydrotheca and the development of the horn this species is intermediate between *C. unicornus* Millard, where the internode and its septa are not involved in the curvature, and *C. dofleini* (Stechow), where the curvature is extreme and practically all the septa are involved. *C. natalensis* also differs from *C. dofleini* in the greater number of internodal septa, in the shorter distal part of the internode and in the longer and septate nematothecae on the phylactocarp.

Cladocarpus sinuosus Vervoort, 1966

Fig. 9A–C

Cladocarpus sinuosus Vervoort, 1966: 155, figs 55–57. Millard, 1975: 428, fig. 132E–H.

Description

These colonies provide further information on the variability of this interesting species.

One colony (Station SM 86) consists of about fifty stems reaching a maximum height of 38 mm. The hydrocladia have thick perisarc with up to ten internodal septa and the hydrothecae are more strongly bent than in previous descriptions. In some of the hydrothecae an abcauline intrathecal septum occurs at a slightly lower level than the adcauline one, reminiscent of *C. leloupi* Millard; hydrothecae both with and without the abcauline septum may occur on the same stem.

Phylactocarps occur in this sample, bearing many oval gonothecae on their inner surfaces between the origins of the nematothecae. The gonothecae have broad subterminal apertures.

Another colony (Station SM 103) consists of a single infertile stem of 10 mm with only a few hydrocladia remaining. It clearly belongs to Vervoort's var. *edentatus*, although a very short abcauline marginal tooth does occur in some of the distal hydrothecae. An interesting feature of this colony is the presence of a short longitudinal septum against the concavity of the abcauline thecal wall of some hydrothecae, reminiscent of *C. paries* Millard.

DISCUSSION

It is not intended to discuss the geographic distribution of the species from this area in any detail at present, since a forthcoming paper will deal with the distribution of the whole of the southern African hydroid fauna utilizing many more records. It may, however, be mentioned in passing that the deep-water hydroids from off the Natal coast appear to be of an extremely mixed nature, including endemic, cosmopolitan, tropical and temperate species with no particular bias to any one component and no clear pointers to the origin of the fauna.

ACKNOWLEDGEMENTS

Financial assistance from SANCOR (The South African National Council for Oceanographic Research) towards the cost of ship's time is gratefully acknowledged, and also the willing and helpful co-operation of all members of the crew of the *Meiring Naude*.

I should also like to express thanks to the British Museum (Natural History) for the loan of slide material for comparison.

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Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (figs 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

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full stop separates references by different authors
figures of plates are enclosed in parentheses to distinguish them from text-figures
dash, not comma, separates consecutive numbers

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33°51′S 25°39′E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

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e.g. '. . . the Figure depicting *C. namacolus* . . .'; '. . . in *C. namacolus* (Fig. 10) . . .'

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Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

N. A. H. MILLARD

THE SOUTH AFRICAN MUSEUM'S *MEIRING NAUDE* CRUISES

PART 3

HYDROIDA

VOLUME 73 PART 6 JUNE 1977 ISSN 0303-2515

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Major headings of the paper are centred capitals; first subheadings are shouldered small capitals; second subheadings are shouldered italics; third subheadings are indented, shouldered italics. Further subdivisions should be avoided, as also enumeration (never roman numerals) of headings and abbreviations.

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Only generic and specific names should be underlined to indicate italics; all other marking up should be left to editor and publisher.

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All illustrations, whether line drawings or photographs, should be termed figures (plates are not printed; half-tones will appear in their proper place in the text) and numbered in a single series. Items of composite figures should be designated by capital letters; lettering of figures is not set in type and should be in lower-case letters.

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PART 4
ECHINODERMS

By

AILSA M. CLARK

Cape Town Kaapstad

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AILSA M. CLARK

British Museum (Natural History), London

[*MS. accepted 15 February 1977*]

ABSTRACT

This paper lists the echinoderm species recently collected in deep water off Natal and is annotated to indicate the eighteen new records for the South African area and the resultant extensions of range. Notes are also given to distinguish the additional species from those keyed and described in a recent paper.

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INTRODUCTION

The material upon which this report was based was collected by the *Meiring Naude* during 1975 and 1976 between 26°50'S and 29°13'S off Natal at depths mostly between 500 and 1 300 metres. Further details of the Station List will be found in the first paper of this series (Louw 1977). One holothurian was inadvertently included (pressed against an echinothuriid). Otherwise the collection consists mainly of ophiuroids, with smaller numbers of asteroids, echinoids and crinoids.

Having just completed what was thought to be a comprehensive survey of the echinoderm fauna of southern Africa south of Capricorn, except for holothurians (Clark & Courtman-Stock 1976), it was disillusioning to find that no less than 10 species of ophiuroids, 5 of asteroids, 2 echinoids and the 1 holothurian are new to the fauna of this area. Most, if not all, of these new records are extensions of range from the Indo-West Pacific, which was to be expected from our previous knowledge of the distribution of the echinoderms of south-east Africa. Unfortunately, positive identifications could not be given for all the additional species because of inadequacy of material, notably for four of the starfish species. Hopefully this situation will soon be resolved by further collections.

Ann. S. Afr. Mus. **73** (6), 1977: 133–147.

Apart from the records of species new to southern Africa, this material also provides minor extensions of range, both horizontal and vertical, for species already cited in the main faunal study.

In the list of species collected that follows, new records for southern Africa (south of the Tropic of Capricorn) are marked *. The latitude/longitude degree grid references and extensions of depth range are given to supplement those in Clark & Courtman-Stock (1976).

LIST OF THE SPECIES COLLECTED

Class CRINOIDEA

Democrinus chuni (Döderlein, 1907)
Sts SM 16, 53, 61, 75, 78, 86, 94, 103 and 109, 384–1 300 metres, 46 specimens.
Grid additions: 28/32/vd, 26/33/vd (vd = very deep, 500+ metres).
Crotalometra magnicirra (Bell, 1905)
St. SM 86, 550 metres, 2 specimens. Grid addition: 27/32/vd.
Antedonid sp. indet.
Sts SM 38, 66, 86 and 107, 550–1 000 (?1 200) metres, 4 poor specimens.

Subclass ASTEROIDEA

Astropecten leptus H. L. Clark, 1926
St. SM 83, 810–600 metres, 1 specimen. Grid addition: 28/32/vd; depth range extended from 375 metres.
Persephonaster roulei euryplax Mortensen, 1933
St. SM 71, 1 050 metres, 1 specimen. Grid addition: 27/33/vd; depth range extended from 410 metres.
Astropectinid sp. juv. ?*P. roulei euryplax* or *Psilaster acuminatus* Sladen, 1889
St. SM 66, 780–720 metres, 1 specimen. (R = 22 mm).
**Cheiraster triplacanthus* Fisher, 1913
St. SM 71, 1 050 metres, 3 specimens. Grid reference: 27/33/vd.
Previously known from the Moluccas.
**Pseudarchaster* sp. aff. *P. myobrachius* Fisher, 1906
St. 72, 1 050 metres, 1 specimen.
P. myobrachius is known from the Hawaiian Islands.
Calliaster acanthodes H. L. Clark, 1923
SAM–A22780, Tugela Bank, 1/4/1974, coll. O.R.I., 1 specimen. (Not from *Meiring Naude* collection.)
**Henricia* sp. ?*H. microplax* Fisher, 1917
St. SM 86, 550 metres, 1 specimen.
H. microplax is known from the Philippine Islands.
**Solaster* sp. aff. *S. paxillatus* Sladen, 1889 and *S. tropicus* Fisher, 1913
Sts SM 44 and 66, 720–768 (?780) metres, 2 specimens.
S. paxillatus is known from south-east Japan to Alaska and *S. tropicus* from the Moluccas.
Hymenaster sp. indet.
St. SM 107, 1 200–1 000 metres, 3 poor specimens.
Pteraster or *Diplopteraster* sp. indet.
St. SM 66, 780–720 metres, 1 poor specimen.
**Zoroaster* sp.
St. SM 107, 1 200–1 000 metres, 1 poor specimen.
Eight species of *Zoroaster* have been recorded from the Indian Ocean.

Subclass OPHIUROIDEA

Ophioscolex dentatus forma *spiniger* Mortensen, 1933
Sts SM 16 and 23, 384 (?376)–400 (?450) metres, 5 specimens.

Amphilimna ? sp.
St. SM 53, 720 metres, 1 poor specimen.
Ophiacantha baccata Mortensen, 1933
Sts SM 23 and 86, 450 (?400)–550 metres, 23 specimens. Depth range extended from 440 metres.
Ophiacantha striolata Mortensen, 1933
St. SM 23, 450–400 metres, 1 poor specimen. Grid addition: 27/32/d (d = 100–499 metres).
**Ophiolimna ?perfida* (Koehler, 1904)
St. SM 77, 780 metres, 1 poor specimen. Grid reference 27/32/vd.
O. perfida is known from Indonesia to southern Japan.
**Ophiophthalmus relictus* (Koehler, 1904)
Sts SM 43(?), 60(?), 66(?), 74 and 107, 420 (?360) – 1 000 (?1 200) metres, 26 specimens, 17 of them small and not positively identifiable. Grid references 28/32/vd, 27/32/vd.
Previously known from the Gulf of Aden, Timor and southern Japan.
**Ophioplinthaca papillosa* H. L. Clark, 1939
St. SM 107, 1 200–1 000 metres, 2 specimens. Grid reference: 28/32/vd.
Previously known from the Gulf of Aden and the Maldive area.
**Ophioplinthaca rudis* (Koehler, 1897)
Sts SM 58, 66, 71, 74, 90 and 107, 780 (?720) – 1 050 (?1 200) metres, 72 specimens. Grid references: 28/32/vd, 27/32/vd, 27/33/vd.
Previously known from the Zanzibar area to Timor and southern Japan.
Ophiothamnus remotus forma *cordatus* Mortensen, 1933
Sts SM 16, 23, 60, 78, 86 and 103, 384 (?376) – 800 (?810) metres, 94 specimens. Grid additions: 28/32/vd, 27/32/vd; depth range extended from 457 metres.
Ophiotreta durbanensis (Mortensen, 1933)
Sts SM 23 and 86, 450 (?400) – 550 metres, 5 specimens. Grid addition: 27/32/vd; depth range extended from 450 metres.
**Ophiotreta matura* (Koehler, 1904)
Sts SM 22, 77(?) and 107, 700 (?492) – 1 000 (?1 200) metres, 3 specimens. Grid references: 28/32/vd, 27/32/vd.
Ophiotreta sp. aff. *O. matura* (Koehler)
St. SM 92, 720–650 metres, 1 small specimen.
Ophiotreta sp. indet.
Sts SM 66 and 67, 680–780 metres, 3 poor specimens.
Amphiura albella Mortensen, 1933
St. SM 67, 700–680 metres, 7 specimens. Grid addition: 27/32/vd; depth range extended from 412 metres.
Amphiura grandisquama natalensis Mortensen, 1933
Sts SM 16, 38, 60, 86 and 103, 384 (?376) – 800 (?825) metres, 33 specimens. Grid additions: 28/32/vd, 27/32/d, vd.
**Amphiura* sp. aff. *A. atlantica* Ljungman, 1867
Sts SM 53 and 60, 720–800 (?810) metres, 13 small specimens.
Amphipholis squamata (Delle Chiaje, 1828)
Sts SM 78, 86, 94 and 103, 550–750 metres, 11 small specimens. Grid additions: 28/32/vd, 27/32/vd; depth range in South Africa extended from 172 metres.
Amphilepis scutata Mortensen, 1933
Sts SM 53 and 60, 720–800 (?810) metres, 4 specimens. Grid additions: 27/32/vd, 26/33/vd; depth range extended from 410 metres.
**Histampica duplicata* (Lyman, 1875)
Sts SM 66, 77 and 103, 680–780 metres, 5 specimens. Grid references: 28/32/vd, 27/32/vd.
Previously known from the tropical West Atlantic and East and West Pacific.
Ophiothrix aristulata Lyman, 1879
Sts SM 16(?) and 23, 384 (?376) – 400 (?450) metres, 3 small specimens. Grid addition: 27/32/d.
**Anophiura simplex* H. L. Clark, 1939
St. SM 53, 720 metres, 1 specimen. Grid reference: 26/33/vd.
Previously known from south of Arabia.
**Aspidophiura corone* Hertz, 1927
Sts SM 31, 53, 60 and 78, 720–800 (?810) metres, 56 specimens. Grid references: 28/32/vd, 27/32/vd, 26/33/vd.
Previously known from off equatorial east Africa.

Astrophiura permira Sladen, 1879
Sts SM 16, 23, 60, 86, 94, 103 and 109, 384 (?376) – 1 300 metres, 74 specimens. Grid additions: 28/32/vd, 27/32/vd; depth range extended from 376 metres.
**Homalophiura schmidtotti* (Hertz, 1927) comb. n.
St. SM 38, 775–825 metres, 1 specimen. Grid reference: 28/32/vd.
Previously known from off equatorial east Africa and Indonesia.
Ophiura flagellata (Lyman, 1878)
St. SM 107, 1 200–1 000 metres, 8 specimens. Grid addition: 28/32/vd.
Ophiurid sp. juv. ? *Homalophiura* sp.
St. SM 109, 1 300 metres, 1 small specimen.
Ophiopallas paradoxa Koehler, 1904
St. SM 16, 376–384 metres, 1 small specimen.

Class ECHINOIDEA

Araeosoma paucispinum H. L. Clark, 1924
St. SM 15, 454–280 metres, 3 specimens.
Phormosoma bursarium A. Agassiz, 1881
Sts SM 22, 38, 53 and 107, 700 (?492) – 1 000 (?1 200) metres, 7 specimens. Grid additions: 28/32/vd, 26/33/vd; depth range extended from 840 metres.
Temnopleurus reevesi (Gray, 1855)
St. SM 23, 450–400 metres, 1 small specimen. Grid addition: 27/32/d; depth range extended from 102 metres.
**Echinocyamus scaber* forma *subconicus* Mortensen, 1948
Sts SM 15, 23, 60, 69, 78, 86 and 103, 450 (?280) – 800 (?810) metres, 30 specimens. Grid references: 28/32/vd, 27/32/d, vd.
Forma *subconicus* previously known from the Kei Islands, Indonesia but *E. scaber* from off equatorial east Africa to south-east Australia and the Hawaiian Islands.
**Gymnopatagus magnus* A. Agassiz & H. L. Clark, 1907
St. SM 107, 1 200–1 000 metres, upper side only of 1 specimen. Grid reference: 28/32/vd.
Previously known from the Andaman Islands to Indonesia and Japan.

Class HOLOTHURIOIDEA

**Orphnurgus glaber* Walsh, 1891
St. SM 107, 1 200–1 000 metres, 1 specimen (squashed against an echinothuriid in preservation).
Previously known from the Bay of Bengal to Japan and the Hawaiian Islands.

SYSTEMATIC SECTION

Class CRINOIDEA

Family **Thalassometridae**

Crotalometra magnicirra (Bell)

Antedon magnicirra Bell, 1905: 141, pl. 4.
Crotalometra magnicirra: Gislén, 1938: 17–18. A. H. Clark, 1950: 97–100. A. M. Clark, 1974: 427–429. A. M. Clark & Courtman-Stock, 1976: 18.

St. SM 86, 27°59,5′S 32°40,8′E, 550 metres, 2 specimens.

One specimen is small. The other has arm length 70+ mm, probably *c.* 100 mm. The high rugose centrodorsal is 4,6 mm high, the breadth (obscured by the cirri) approximately the same.

The specimen is unusual in having 6 out of the 7 second division (IIBr) series present with only 2 ossicles rather than the 4 characteristic of the genus *Crotalometra*. Only a single such short IIBr series was found in all 16 specimens of the type series studied in 1974, though Gislén (1938) found 4 out of 10 such series in one of his specimens.

The mature cirri number *c.* XXVII, with *c.* vii immature ones, arranged in 10 columns of usually 3 cirri, separated into 5 pairs of columns by narrow triangular bare radial areas, as in the type series. Two intact peripheral cirri have 68 and 66 segments, the maximum otherwise recorded for this species being 64; also the seventh segment is the transition one, rather than the ninth or tenth. The closely appressed division series are finely rugose laterally, where the syntypes are smooth.

Finally the first pinnule (which is P_1 in this case since the IIBr series have only two ossicles) has 29+ *c.* 2 segments and measures just over 14 mm, compared with up to 27 segments and *c.* 12 mm length in P_D of the syntype described in 1974; otherwise the shape is similar.

Despite these small differences, there does not appear to be sufficient justification for regarding this sample as specifically distinct from *Crotalometra magnicirra*, especially considering the geographical approximation, the nearest previous record for the species being *c.* 29,5°S 31,5°E.

Of the two other species of *Crotalometra*, *C. rustica*, known from the Bay of Bengal to Indonesia, and *C. sentifera*, from the Maldive area, both have the brachials beyond the arm bases more or less markedly produced and spinose at their distal edges.

Antedonidae sp(p). indet.

St. SM 38, 28°21,9'S 32°34,6'E, 775–825 metres, 1 broken specimen.
St. SM 66, 27°17,5'S 32°54,1'E, 780–720 metres, 1 small specimen.
St. SM 86, 27°59,5'S 32°40,8'E, 550 metres, 1 small specimen.
St. SM 107, 28°37,8'S 32°38,4'E, 1 200–1 000 metres, 1 small specimen.

The best of these specimens, from station SM 107, at least seems to have some affinity with *Tonrometra* of the subfamily Bathymetrinae except that P_1 is smaller than P_2 or P_3, not larger. The centrodorsal is low conical and there is some tendency for arrangement of the sockets in vertical rows. The cirrus segments number up to 25, the distal ones short and keeled dorsally. The division series and brachials have spinose distal edges.

Class STELLEROIDEA

Subclass ASTEROIDEA

Family **Astropectinidae**

Astropecten leptus H. L. Clark

Astropecten leptus H. L. Clark, 1926: 6–8, pl. 1 (figs 3–4). Mortensen, 1933: 234, pl. 9 (figs 3–4). Madsen, 1950: 169. Cherbonnier & Nataf, 1973: 1268–1272, fig. 8A–F, pl. 12. A. M. Clark & Courtman-Stock, 1976: 51.

St. SM 83, 28°00,5'S 32°46,4'E, 810–600 metres, 1 specimen.

R/r (the major to minor radius) = 40/8 mm = 5,0/1, compared with 59/11 mm = 5,3/1 in the holotype of *A. leptus* from off Durban in 287–348 metres. This specimen differs in having no enlarged superomarginal spines, the occurrence of which is variable in most species of *Astropecten*. It also has 3 actinal plates each side of the interradius compared with 2 in the holotype, though Madsen found up to 4 and Cherbonnier and Nataf up to 5 in their specimens from West Africa.

Family **Benthopectinidae**

Cheiraster triplacanthus Fisher

Cheiraster triplacanthus Fisher, 1913: 206. Fisher, 1919: 205–208, pl. 48 (figs 3–4), pl. 55 (figs 1, 1a).

St. SM 71, 27°21,3′S 33°03,9′E, 1 050 metres, 3 specimens.

In the asteroid key of Clark & Courtman-Stock (1976: 33) this species runs down to *Luidiaster hirsutus* from which it differs in the greater extent of the superomarginal plates on the upper side and the triple distal superomarginal spines.

This record represents an extension of range from Celebes in the Moluccas in 1 280 metres, only the holotype being known hitherto.

The largest specimen has R/r 42/9 mm = 4,7/1, compared with 49/12 mm = 4,1/1 in the holotype. The two or three up and inwardly directed slightly curved superomarginal spines on each plate near the arm tips, characteristic of the species, are very distinctive; also the subambulacral spines are not at all enlarged. The bilobed papularia each have *c*. 35 pores, whereas Fisher estimated *c*. 80 in the holotype.

Family **Goniasteridae**

Pseudarchaster sp. aff. *P. myobrachius* Fisher, 1906

See: Fisher 1906: 1037.

St. SM 72, 27°17,8′S 33°04,5′E, 1 050 metres, 1 specimen.

R/r = 44/16 mm = 2,8/1. This ratio is intermediate between those cited in Clark & Courtman-Stock (1976: 35) of 3/1 or more for *P. tessellatus* Sladen, 1889 and 2,0–2,7/1 for the shorter-armed *P. brachyactis* H. L. Clark, 1923, already known from southern Africa but not on the south-east side. Recent studies by Halpern (unpublished thesis on the family Goniasteridae) indicate that the range of variation in the proportions of *Pseudarchaster* species is much greater than has previously been supposed. However, there are also a number of morphological differences between this specimen and *P. tessellatus*.

These include the smaller number of marginal plates, 26 in each series compared with *c*. 35 in *tessellatus* of similar R, the capitate rather than tapering form of the relatively short armament of the actinal plates and the absence of enlarged spinelets on these plates, as well as the shortness of the spines on the interradial inferomarginals. These two last characters agree with *P. myobrachius* Fisher, 1906, in which R/r of the holotype is 2,6/1 and there are 23 superomarginals in each series at R 34 mm. However, that species has been recorded only from the Hawaiian Islands (in 780–1 240 metres).

Family **Echinasteridae**

Henricia sp. ? *H. microplax* Fisher, 1917

See: Fisher 1919: 437.

St. SM 86, 27°59,5'S 32°40,8'E, 550 metres, 1 specimen.

Among the three species of *Henricia* from southern Africa cited in the asteroid key of Clark & Courtman-Stock (1976: 42), this specimen differs from *H. abyssalis* in the more solid opaque spinelets and from *H. retecta* and *H. ornata* in the more compact skeleton and the multiple series of spinelets on the adambulacral and actinal plates.

It agrees with *H. microplax* Fisher, from the Philippines, in the fine and very compact skeleton with only single papulae in the individual meshes, the relatively conspicuous inferomarginal plates (at least in the proximal half of the arm) with two or three series of intermarginal plates separating them near the arm base from the smaller superomarginal series and the multiple series of subambulacral spines. Proximally there are no papulae below the superomarginals but in the distal half of the arm where the plate arrangement is more irregular the papulae approximate to the adambulacrals.

Family **Solasteridae**

Solaster sp. aff. *S. paxillatus* Sladen, 1889 and *S. tropicus* Fisher, 1913

Solaster sp., possibly *S. paxillatus* Sladen or *S. tropicus* Fisher, A. M. Clark & Courtman-Stock, 1976: 40 (footnote).

See: Sladen 1889: 452; Fisher 1919: 444.

St. SM 44, 29°40,6'S 32°32,5'E, 722–768 metres, 1 specimen.

St. SM 66, 27°17,5'S 32°54,1'E, 780–720 metres, 1 small specimen.

In comparison with the multiradiate South African solasterid *Crossaster penicillatus* Sladen, 1889, the skeleton of these two eight-armed specimens is much finer and more compact. Their affinities lie with *S. paxillatus* from south-east Japan and *S. tropicus* from the Moluccas, which are closely related. The holotypes of both have nine arms, but Fisher (1911) found additional North Pacific specimens of *S. paxillatus* to have eight to ten arms.

Subclass OPHIUROIDEA

Family **Ophiacanthidae**

Ophiolimna sp. ? *O. perfida* (Koehler, 1904)

See: Koehler 1922: 64.

St. SM 77, 27°31,6'S 32°50,0'E, 780 metres, 1 specimen.

In the ophiuroid key of Clark & Courtman-Stock (1976: 121) this specimen cuts across dichotomy no. 68, having the apical oral papilla (or pair of papillae) somewhat blunted and a very broad fourth oral papilla present each side, coupled with very large lateral arm plates. The distal oral papilla, the relatively broad, rounded single tentacle scale and the coarse granules on the oral plates serve to distinguish it from the other South African Ophiacanthidae. It agrees with *Ophiolimna perfida* Koehler from the Philippines and Indonesia in the coarse granules on the oral plates, the operculiform distal oral papilla overlying the second oral tentacle scale, the very long and quite smooth arm spines and the single large rounded tentacle scale. The only difference noted is that the disc spines are more elongate than usual in *O. perfida*, the height sometimes exceeding twice the breadth (compare Koehler 1922, pl. 92 (fig. 6)).

Ophiophthalmus relictus (Koehler)

Ophiacantha relicta Koehler, 1904: 106–107, pl. 17 (figs 4–6).
Ophiophthalmus relictus: Koehler, 1922: 124–127, pl. 9 (figs 1–4), pl. 95 (fig. 3). H. L. Clark, 1939: 54–55.

St. SM 43, 28°45,5′S 32°24,5′E, 420–360 metres, 10 specimens.
St. SM 60, 27°09,6′S 32°58,2′E, 800–810 metres, 6 small specimens (?*relictus*).
St. SM 66, 27°17,5′S 32°54,1′E, 780–720 metres, 1 small specimen (?*relictus*).
St. SM 74, 27°38,6′S 32°52,6′E, 860 metres, 1 specimen.
St. SM 107, 28°37,8′S 32°38,4′E, 1 200–1 000 metres, 8 specimens.

This species cuts across dichotomy no. 69 in the 1976 key, having moderately large but well-separated radial shields; this character, together with the granules bordering the dorsal arm plates, serves to distinguish it from the other ophiacanthids of southern Africa.

The disc scaling is just distinct between the low spaced rugose granules. In the smaller specimens the granules tend to be limited to the edges of the scales. The bare radial shields are separated by about their own breadth. The dorsal arm plates are rhombic or slightly bell-shaped, usually with bead-like granules along their distal edges. The arm spines are only finely rugose and relatively short, only the uppermost of the six on the first two free segments exceeding the segment in length.

Ophioplinthaca papillosa H. L. Clark

Ophioplinthaca papillosa H. L. Clark, 1939: 49–51, figs 10–11.

St. SM 107, 28°37,8′S 32°38,4′E, 1 200–1 000 metres, 2 specimens.

This species cuts across dichotomy no. 75 in the 1976 key, having five arms but the distalmost oral papilla papilliform. Apart from the number of arms, it differs from *Ophioplinthaca sexradia* in having very long arm spines.

The holotype of *O. papillosa* was collected at the same John Murray Expedition station in the Gulf of Aden at 1 270 metres as a specimen of *O. rudis* (Koehler) and off Natal the two still appear to be sympatric. Although both species have the interradially creased disc and large bare radial shields characteristic of the genus, *O. rudis* has the radial shields separated and the disc spinelets (if present) slender, whereas in *O. papillosa* the radial shields are more or less broadly contiguous and the armament is in the form of short stumps with thorny crowns, also the oral papillae of *O. rudis* are much more numerous and irregular than the three each side of *O. papillosa*.

Ophioplinthaca rudis (Koehler)

Ophiomitra rudis Koehler, 1897: 358, pl. 9 (figs 74–75).
Ophioplinthaca rudis: Koehler, 1922: 142–147, pl. 24 (figs 1–6), pl. 96 (fig. 1). H. L. Clark, 1939: 46–47.

St. SM 58, 27°09,7'S 33°01,0'E, 850–790 metres, 2 specimens.
St. SM 66, 27°17,5'S 32°54,1'E, 780–720 metres, 1 specimen.
St. SM 71, 27°21,3'S 33°03,9'E, 1 050 metres, 3½ specimens.
St. SM 74, 27°38,6'S 32°52,6'E, 860 metres, 8½ specimens.
St. SM 90, 28°09,8'S 32°47,4'E, 940 metres, 3 specimens.
St. SM 107, 28°37,8'S 32°38,4'E, 1 200–1 000 metres, 54 specimens.

This species falls with difficulty into the Ophiacanthidae as defined in dichotomy no. 68 of the 1976 key, since the oral papillae are numerous and irregular, though the large lateral arm plates and the long arm spines should indicate this family. Also the radial shields, though large and bare, are not contiguous, thus blurring the division of no. 69. Other comments on the distinction of *O. rudis* are given under *O. papillosa* above.

Ophiotreta matura (Koehler)

Ophiacantha matura Koehler, 1904: 112–113, pl. 23 (figs 2–4).
Ophiotreta matura: Koehler, 1922: 76–81, pls 12–14, pl. 15 (figs 1–3). H. L. Clark, 1939: 53–54. A. M. Clark & Courtman-Stock, 1976: 1, 121 (footnotes).

St. SM 22, 27°45,0'S 32°44,8'E, 700–492 metres, 1 specimen.
St. SM 77, 27°31,6'S 32°50,0'E, 780 metres, 1 specimen.
St. SM 107, 28°37,8'S 32°38,4'E, 1 200–1 000 metres, 1 specimen.

This species too has multiple and irregular oral papillae but the large lateral arm plates ally it with this family. It is distinguished from *Ophiotreta durbanensis* in a footnote on p. 121 of the 1976 key.

Ophiotreta sp. aff. *O. matura* (Koehler)

See: Koehler 1922: 76.

St. SM 92, 28°14,5'S 32°40,6'E, 720–650 metres, 1 small specimen.

Whereas preserved specimens of *Ophiotreta matura* usually retain (or show) a dark colouration of the arm spines, this specimen is white throughout and the spines are transparent. They are also much more thorny than in *O. matura* and even the tentacle scales are thorny. The long disc spinelets form a dense coat; they end in several thorns. The lowest arm spine becomes hooked on the distal segments, as also in *O. matura*.

Family **Amphiuridae**

Amphiura sp. aff. *A. atlantica* Ljungman, 1867

See: Mortensen 1933: 351.

St. SM 53, 26°51,1′S 33°12,5′E, 720 metres, 2 specimens.

St. SM 60, 27°09,6′S 32°58,2′E, 800–810 metres, 11 small specimens.

The largest specimen, from station 53, has d.d. (disc diameter) 4,5–5,0 mm, the radial shields are completely separate, equal in length to about half the disc radius, the disc scaling is rather deficient ventrally, the oral plates have an almost superficial flange bearing the first oral tentacle scale, the distal oral papilla is spiniform, the consecutive dorsal arm plates are narrowly separated by the lateral arm plates, there are five arm spines proximally, the lower ones tending to be slightly truncated and even a little bihamulate with a suggestion of a distal hook and there is one small tentacle scale. The reduced ventral scaling, the modified arm spines and the small tentacle scale agree with *Amphiura atlantica*, to which species it runs down in the 1976 key; also the smaller specimens (d.d. up to only 2 mm) do have the radial shields just contiguous and lack tentacle scales altogether, which may be true of *A. atlantica*. However, the flanged oral plates are quite distinct, approximating to those of *Amphilepis*, which is ranged in a separate subfamily of Amphiuridae. They are shared by *Amphiura pycnostoma* H. L. Clark, 1911, from south-east Japan but that species has the distal oral papilla papilliform, the successive dorsal arm plates contiguous and only three arm spines. The holotype of *A. pycnostoma* has one small tentacle scale.

Family **Ophiactidae**

Histampica duplicata (Lyman)

Amphiura duplicata Lyman, 1875: 19, fig. 87, pl. 5 (fig. 78). Lyman, 1882: 136, pl. 17 (figs 10–12).
Amphiactis duplicata: Koehler, 1922: 204–205, pl. 63 (figs 1–4).
Histampica duplicata: A. M. Clark, 1970: 73.

St. SM 66, 27°17,5′S 32°54,1′E, 780–720 metres, 2 specimens.

St. SM 77, 27°31,6′S 32°50,0′E, 780 metres, 1 specimen.

St. SM 103, 28°31,7′S 32°34,0′E, 680 metres, 2 specimens.

This species, currently included in the Ophiactidae, may not run down to that family in dichotomy no. 60 of the 1976 key since its apical oral papilla is not markedly broadened and is in series with several lateral oral papillae each side. Difficulty may also arise at no. 68 since the oral structure may be confused with that of some ophiacanthids. The very coarse, well-defined, naked disc scales, separate radial shields, smooth and not excessively long arm spines, two tentacle scales and usual subdivision transversely of the proximalmost ventral arm plate into two, should serve to distinguish *Histampica duplicata*.

It is likely that this species will prove to be cosmopolitan.

Family **Ophiuridae**

Anophiura simplex H. L. Clark

Anophiura simplex H. L. Clark, 1939: 119–121, figs 55–56.

St. SM 53, 26°51,1′S 33°12,5′E, 720 metres, 1 specimen.

In the 1976 key* this species cuts across dichotomy no. 102, since only the first three pairs of pores are present on each arm but the pores of the first segment have more than one scale. The unique holotype of *A. simplex*, from the south Arabian coast, had lost its oral papillae, which are intact on this specimen and are close-fitting and rectangular, like those of *Anophiura planissima* H. L. Clark, 1939, from the Gulf of Aden. The absence of arm combs distal to the radial shields, the thin disc with a single large interradial plate between the neighbouring radial shields and the reduction of the tentacles after the basal pores should serve to distinguish this species from the others known from southern Africa.

The Natal specimen has d.d. 6,0 mm and a.l. (arm length) 10+1 or 2 mm, so that a.l./d.d. probably does not exceed 2/1, confirming H. L. Clark's estimate that the arms of *A. planissima* are more attenuated at a ratio of *c*. 2,5/1 than those of *A. simplex*. The matt, rather than shiny, surface texture and the prolonged lateral angles of the proximal ventral arm plates also agree with *A. simplex* rather than *A. planissima*.

Aspidophiura corone Hertz

Aspidophiura corone Hertz, 1927: 79–80, pl. 7 (figs 1–2).

St. SM 31, 28°04,5′S 32°42,8′E, 740 metres, 1 small specimen.
St. SM 53, 26°51,1′S 33°12,5′E, 720 metres, 16 specimens.
St. SM 60, 27°09,6′S 32°58,2′E, 800–810 metres, 35 specimens.
St. SM 78, 27°31,6′S 32°50,0′E, 750 metres, 4 specimens.

Like *Anophiura simplex*, this species has reduced tentacle pores and single large interradial disc scales between the radial shields, but it differs in having well-developed spiniform arm combs distal to the radial shields and the rosette of primary disc plates very conspicuous, fully contiguous and with a distinct boss on the central plate.

Astrophiura permira Sladen

Astrophiura permira Sladen, 1879: 401–415, pl. 20. Hertz, 1927: 83–85, pl. 7 (figs 4–5). Mortensen, 1933: 394–396, figs 90–91. A. M. Clark & Courtman-Stock, 1976: 188.

St. SM 16, 27°33,0′S 32°44,6′E, 384 metres, 17 specimens.
St. SM 23, 27°44,4′S 32°42,8′E, 450–400 metres, 10 specimens.
St. SM 60, 27°09,6′S 32°58,2′E, 800–810 metres, 22 specimens.
St. SM 86, 27°59,5′S 32°40,8′E, 550 metres, 5 specimens.

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* Note an error in dichotomy 93 of the 1976 key (Clark & Courtman-Stock 1976: 124) in which the second alternative should lead to no. 101, not 100.

St. SM 94, 28°16,3′S 32°38,8′E, 670 metres, 2 specimens.
St. SM 103, 28°31,7′S 32°34,0′E, 680 metres, 17 specimens.
St. SM 109, 28°41,0′S 32°36,8′E, 1 300 metres, 1 specimen.

The arms of this species are almost invariably broken but a very few of these are intact. A very young complete specimen with the true disc diameter (less the marginal fringe) 1,1 mm and the expanded disc diameter 1,7 mm, has a free arm of five segments (the first segment becoming incorporated into the disc) measuring 1,7 mm in length. A larger specimen with expanded disc diameter 4,5 mm has a complete arm of eight free segments measuring 2,5 mm to the edge of the marginal fringe. The terminal ossicle is slightly tapering but otherwise almost cylindrical. At this size, there are five pairs of podia within the disc. A detached complete free arm of sixteen segments measures 6,5 mm. The maximum known expanded disc diameter in this species is 14 mm.

Homalophiura schmidtotti (Hertz) comb. n.

Ophiuroglypha schmidt-otti Hertz, 1927: 91–93, fig. 5, pl. 7 (figs 11–12).

St. SM 38, 28°21,9′S 32°34,6′E, 775–825 metres, 1 specimen.

Mortensen (1933) reduced *Ophiuroglypha* Hertz to the rank of a subgenus of *Ophiura* but restored it in 1936 (Mortensen 1936: 316) when dealing with the type species, *Ophioglypha lymani* Ljungman, 1870. The main distinction of *Ophiuroglypha* was a modification of the middle one of the three arm spines on the distal segments into an outwardly turned hook. Comparison of *O. schmidtotti* with *O. lymani* shows marked differences. *O. lymani* has relatively longer, markedly carinate arms, with the successive dorsal arm plates quite broadly contiguous, the arms straight-sided, a much smoother disc, discrete apical oral papillae and tentacle pores extending to about the twelfth arm segment. Conversely, there is a close resemblance between *O. schmidtotti* and *Ophioglypha inornata* Lyman, 1878, the type-species of *Homalophiura*. Both have the second oral tentacle pore opening completely outside the oral slit (in *Ophiuroglypha lymani* the pore runs into the oral slit), only four or five proximal arm segments with tentacle pores, the arm combs more or less reduced with short bead-like papillae, the disc and arm plates markedly thickened and the oral papillae and tentacle scales rectangular and very close-fitting. The main difference is the greater number of disc scales and the smaller size of the primaries, which are separated by only single series of relatively large scales in *H. inornata*, an Atlantic species. *H. schmidtotti* is very similar to *Homalophiura glypta* H. L. Clark, 1939, from the Maldive area, especially in the apparently sunken middle parts of the larger disc scales, but these are relatively smaller and have a very shiny texture in *H. glypta*.

In the 1976 key, this species runs down to no. 112 but differs from *Ophiura* (*Ophiuroglypha*) *irrorata* and *costata* in having the radial shields asymmetrically contiguous mid-radially, all the oral papillae rectangular and very close-fitting and the arms markedly moniliform.

The present specimen has d.d. 8,0 mm; the arms are all broken within 10 mm but were probably not more than as long again, so that a.l./d.d. was probably 2,0–2,5/1.

Class ECHINOIDEA

Family **Fibulariidae**

Echinocyamus scaber forma *subconicus* Mortensen

Echinocyamus scaber forma *subconicus* Mortensen, 1948: 188, pl. 46 (figs 34–36).

St. SM 15, 28°31,0′S 32°45,6′E, 454–280 metres, 1 specimen.
St. SM 23, 27°44,4′S 32°42,8′E, 450–400 metres, 1½ specimens.
St. SM 60, 27°09,6′S 32°58,2′E, 800–810 metres, 1 specimen.
St. SM 69, 27°12,2′S 32°56,0′E, 660 metres, 15 specimens.
St. SM 78, 27°31,6′S 32°50,0′E, 750 metres, 2 specimens.
St. SM 86, 27°59,5′S 32°40,8′E, 550 metres, 6 specimens.
St. SM 103, 28°31,7′S 32°34,0′E, 680 metres, 4 specimens.

Several of these specimens were alive when collected and are complete with spines. Their colour in spirit is green. Although the periproct is usually bare of spinelets, one specimen has *c.* 12 periproctal spines and another about 6. This throws some doubt on the weight of this character which is one of those supposed by Mortensen to distinguish the subgenus *Mortonia.* Only *Echinocyamus australis* (Desmoulins), from the Hawaiian and neighbouring Pacific Islands, and *E. polyporus* Mortensen, from New Zealand, were included by Mortensen in *Mortonia.*

The test is usually low rounded subconical, much as in the specimen from the Kei Islands illustrated by Mortensen. Length/breadth/height of one specimen is 7,75/6,80/3,75 mm, l/ht = 2,1/1. In this specimen there are three pore pairs on each side of each petal.

The largest specimen, from station SM 86, is flatter than most, l/br/ht 8,3/7,5/3,0 mm, l/ht = 2,8/1. Its periproct is naked, with relatively few plates. There are four pore pairs on each side of each petal. All the ocular pores on the apical system, except for the posterior one, are enlarged to the same size as the genital pores, as in *Echinocyamus grandiporus* Mortensen from the West Indies and Azores. This last character is not shared by the other specimens.

Echinocyamus scaber runs down to dichotomy no. 43 in the Clark & Courtman-Stock key (1976: 211). It is distinguishable from *Echinocyamus elegans* by the presence of glassy tubercles scattered over the upper side, by the much shorter petals, *E. elegans* having eight or nine pore pairs each side at this size, and by the slightly conical shape.

Family **Brissidae**

Gymnopatagus magnus A. Agassiz & H. L. Clark

Gymnopatagus magnus A. Agassiz & H. L. Clark, 1907: 133. Mortensen, 1951: 447–449, figs 219, 220a, pl. 26 (figs 7–9), pl. 27 (figs 8–10), pl. 61 (figs 19–26).

St. SM 107, 28°37,8′S 32°38,4′E, 1 200–1 000 metres, upper side of one specimen.

In the 1976 key, this species runs down to dichotomy no. 53. It is distinguished from *Spatagobrissus mirabilis* by the well-developed frontal notch in the test and from *Brissopsis lyrifera capensis* by the enlarged aboral primary spines and the shape of the peripetalous fasciole, which is not concave between the petals.

Class HOLOTHURIOIDEA

Family **Deimatidae**

Orphnurgus glaber Walsh

Orphnurgus asper var. *glaber* Walsh, 1891: 198.
Orphnurgus glaber: Hansen, 1975: 39–46, figs 12–13, pl. 8 (figs 5–7).

St. SM 107, 28°37,8′S 32°38,4′E, 1 200–1 000 metres, 1 squashed specimen.

This specimen is in poor condition, completely flattened and bearing the imprint of the echinothuriid against which it was pressed. There are twenty tentacles. Hansen stresses the variability of the spicules in this species. Here they are mostly in the form of rods with branching or ornamented ends, many resembling Hansen's figures 13.30, 41 and 43 but others are shorter and stout with elaborately spiny ends, like some of the spicules of *Orphnurgus asper* Théel, from the West Indies.

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Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

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Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (*Lembulus*) *bicuspidata* (Gould, 1845)

Figs 14–15A

Nucula (*Leda*) *bicuspidata* Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (figs 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

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In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33°51′S 25°39′E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

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(a) The Figures, Maps and Tables of the paper when referred to in the text
e.g. '. . . the Figure depicting *C. namacolus* . . .'; '. . . in *C. namacolus* (Fig. 10) . . .'

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Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

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AILSA M. CLARK

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ECHINODERMS

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(*continued inside back cover*)

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CRETACEOUS FAUNAS FROM ZULULAND AND NATAL, SOUTH AFRICA
THE AMMONITE FAMILY TETRAGONITIDAE HYATT, 1900

By

William James Kennedy
Geological Collections, University Museum, Oxford

&

Herbert Christian Klinger
South African Museum, Cape Town

(With 27 figures)

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ABSTRACT

Members of the Tetragonitidae typically form a minor portion of the ammonite fauna of the South African Cretaceous, being important only in the Upper Campanian and Lower Maastrichtian. The following species are described: *Tetragonites? heterosulcatus* Anthula, *Tetragonites subtimotheanus* Wiedmann, *Tetragonites superstes* Van Hoepen, *Tetragonites* cf. *epigonum* (Kossmat), *Saghalinites cala* (Forbes), *Saghalinites nuperus* (Van Hoepen), *Pseudophyllites indra* (Forbes), *Pseudophyllites teres* (Van Hoepen) and *Pseudophyllites latus* (Marshall). The majority of all these forms are widely distributed circum-indic species, but *T. ? heterosulcatus* has been previously recorded only from Daghestan, the Caucasus, Bulgaria and Tunisia. The material allows a revision of the poorly known *T. superstes*, *S. nuperus* and *P. teres*, whilst *T. virgulatus* van Hoepen is confirmed as a synonym of *P. indra*. Ontogenetic series of *T. subtimotheanus* are illustrated, as is the ontogeny and variation in *S. cala*. This latter material shows a range of ventral ridges and striations associated with the ventral lobe and siphuncle of unknown function.

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INTRODUCTION

The Tetragonitidae are a small group of ammonites, conservative in external morphology, but showing a progressive, sexlobate suture line with a formula $ELU_2U_3{=}S\ U_1I_S$. The group evolved from the Gaudryceratidae during the Aptian via *Eogaudryceras* (*Eotetragonites*); they range from the Upper Aptian

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to the Lower Maastrichtian, and have a wide distribution, being locally common in areas as far apart as Alaska, New Zealand, Japan and Antarctica. They are, however, rare in the Boreal region; only a few specimens are known from Europe and Asia north of the Alpine fold belts, and none are recorded from the Western Interior of the United States. In South Africa, species are known from the Lower/Middle Albian to Maastrichtian, and are relatively common in the Upper Campanian and Lower Maastrichtian.

The following species are described below:

Tetragonites? heterosulcatus Anthula
Tetragonites subtimotheanus subtimotheanus Wiedmann
Tetragonites superstes Van Hoepen
Tetragonites cf. *epigonum* Kossmat
Saghalinites cala (Forbes)
Saghalinites nuperus (Van Hoepen)
Pseudophyllites indra (Forbes)
Pseudophyllites teres (Van Hoepen)
Pseudophyllites latus (Marshall)

LOCATION OF SPECIMENS

The following abbreviations are used to indicate the source of material:

BMNH	British Museum (Natural History), London
MHNG	Muséum d'Histoire Naturelle, Geneva
EMP	École des Mines, Paris
MHNP	Muséum d'Histoire Naturelle, Paris
SAS	South African Geological Survey, Pretoria
TM	Transvaal Museum, Pretoria
DM	Durban Museum
UPE	University of Pretoria
SAM	South African Museum, Cape Town
NMB	National Museum, Bloemfontein.

FIELD LOCALITIES

Outline details of field localities referred to in this paper are given by Kennedy & Klinger (1975); full descriptions of sections are deposited in the library of the Palaeontology Department of the British Museum (Natural History) and in the Palaeontology departments of the South African Museum and the South African Geological Survey.

DIMENSIONS OF SPECIMENS

All dimensions given below are in millimetres:

D = diameter, Wb = whorl breadth, Wh = whorl height, U = umbilicus.
Figures in parentheses are dimensions as a percentage of the total diameter.

SUTURE TERMINOLOGY

The suture terminology of Wedekind (1916, *see* Kullman & Wiedmann 1970) is followed in the present work:

I_S = internal lobe with septal lobe, U = umbilical lobe, L = lateral lobe, E = external lobe.

SYSTEMATIC PALAEONTOLOGY

Phylum	**MOLLUSCA**
Class	CEPHALOPODA Cuvier, 1797
Subclass	AMMONOIDEA Zittel, 1884
Order	LYTOCERATIDA Hyatt, 1899
Superfamily	TETRAGONITACEAE Hyatt, 1900
Family	**Tetragonitidae** Hyatt, 1900
Genus	*Tetragonites* Kossmat, 1895

Type species

Ammonites timotheanus Pictet (1848: 295, pl. 2 (fig. 6), pl. 3 (fig. 1)) by original designation.

Diagnosis

Moderately evolute tetragonitids characterized by a round to subrectangular whorl section and oblique prorsiradiate constrictions which are typically flexed over the venter and have a distinct concave ventral sinus. Suture formula $ELU_2U_3{=}S\ U_1I_S$. The external lobe (E) is deeper than the first lateral lobe (L); there is an irregularly bifid or trifid termination to the first lateral saddle (E/L) and a nearly symmetrical lateral lobe (L).

Discussion

Tetragonites can be separated from *Saghalinites* Wright & Matsumoto, 1954 on the basis of the more evolute coiling, lower expansion rate and much simpler suture of that genus. *Pseudophyllites* Kossmat, 1895 is much more inflated and involute, has a much higher expansion rate, a typically rounded, frequently compressed whorl section, no constrictions and a reticulate ornament, whilst the suture is far more highly subdivided.

The genus *Epigoniceras* Spath, 1925 with *Tetragonites epigonus* Kossmat, 1895 as type species was proposed for Lower Turonian to Maastrichtian tetragonitids which differed from earlier *Tetragonites sensu stricto* in having a retracted suspensive lobe with a much larger number of auxiliary elements. *Epigoniceras* has been accepted by Usher (1952), Wright & Matsumoto (1954), Wright (1957) and Collignon (1956, 1965*a*, 1965*b*, 1966, 1969), but Howarth (1958: 9) has successfully proved that straight, recurved and even upcurved suspensive lobes are to be found throughout the time range of the group, so that *Epigoniceras* does not bear separation from *Tetragonites* even on a stratigraphic basis. Wiedmann (1973: 609) has introduced the genus *Carinites*, with *Tetragonites* *spathi* Fabre (1940: 214, pl. 6 (fig. 1), text-fig. 26) as type species for tetragonitids with a subrectangular whorl section, persistent, irregularly spaced constrictions projected on the flanks and converging to a marked ventral peak, and a persistent, if feeble ventral keel. Wiedmann regarded the keel as a feature unknown in any other tetragonitid species, but similar 'keels' of this type are quite widespread in the material here present, occurring for instance in *Tetragonites superstes* Van Hoepen (1921: 10, pl. 2 (figs 17–20)). A distinct keel also occurs in *Tetragonites epigonus* Kossmat (e.g. Usher 1952, pl. 2 (fig. 7)) and such features are widely developed in *Saghalinites cala* (Forbes) (p. 168). This feature is not a floored keel, rather it is a raised siphonal area associated with the siphuncle. Rather similar keels are found in many ammonite groups, and appear to be variable features of specific value only, suggesting that *Carinites* may possibly be placed in the synonymy of *Tetragonites.*

Collignon (1956: 98) listed twenty-eight species and varieties of *Tetragonites* and *Epigoniceras* in his review of the genus, and since his work, Aptian to Cenomanian species have been described and discussed by Wiedmann (1962*a*, 1962*b*, 1973), Wiedmann & Dieni (1968) and Murphy (1967*a*, 1967*b*) so that over thirty names are in current usage and there are a number of other named forms, chiefly based on nuclei, which may be synonyms of better known species, or which can only be regarded as *nomen dubia.*

The authors find it difficult to believe that this host of species, many with overlapping or identical geographic and stratigraphic ranges, is indeed a true picture of the evolution of the genus, but the current material is inadequate for a satisfactory critical appraisal of the list.

Occurrence

Tetragonites first appears in the Upper Aptian, and ranges to the Maastrichtian. The genus has an almost world-wide distribution, with records from Antarctica, South Africa, Mozambique, New Zealand, Madagascar, Japan, Sakhalin, Algeria, Tunisia, the western Mediterranean, Spain, southern France, Switzerland, England, northern France, a variety of localities in central Europe, and Sinai. In North America there are records from Texas and northern Mexico, California, Oregon, British Columbia, and Alaska.

Tetragonites? heterosulcatus Anthula, 1899

Figs 1A–F, 2A–B

Lytoceras (*Tetragonites*) *heterosulcatus* Anthula, 1899: 99–100, pl. 7 (fig. 4), *non* pl. 7 (fig. 5). Pervinquière, 1907: 73.

Tetragonites heterosulcatus Drushchits, 1956: 102, pl. 7 (figs 27–28), text-fig. 44; 1960: 260, text-fig. 68. Murphy, 1967*a*: 32, text-fig. 14. Dimitrova, 1967: 31, pl. 11 (figs 1–1a), text-fig. 13.

Type

Lectotype herein designated, the original of Anthula's (1899, pl. 7 (fig. 4)) from the Akusha Shales (Aptian) of Daghestan.

Material

Three specimens, BMNH C78827–C78829, from Bed J of the Mzinene Formation, locality 171, Mlambongwenya Spruit, northern Zululand (Albian II–III).

Dimensions

	D	*Wb*	*Wh*	*Wb/Wh*	*U*
Lectotype (from Anthula)	24,0	13,0(54)	9,0(37)	1,4	8,0(33)
BMNH C78827	49,0	24,8(51)	20,8(42)	1,2	10,9(22)
BMNH C78828	—	23,0(—)	19,0(—)	1,2	—

Description

The coiling is fairly evolute, about 40 per cent of the previous whorl being covered. The whorls expand at a moderate rate, are depressed, and have their greatest thickness below mid-flank. The umbilicus is of moderate size, 22 per cent of the diameter, and fairly deep. The umbilical wall is vertical, the umbilical shoulder abruptly rounded, the flanks flattened and subparallel, the ventrolateral shoulders abruptly rounded, the venter broad and flattened.

The surface of the shell (Figs 1A–C, 2B) bears fine growth striae and strong, flexuous prorsiradiate constrictions, fourteen or fifteen on the outer whorl, each preceded by a fine, low, rounded collar. The constrictions are narrow and quite deeply incised; they arise at the umbilical seam, pass straight up the umbilical wall, sweep forwards across the ventrolateral shoulder and are strongly prorsiradiate and markedly convex across the flanks. They flex backwards across the upper flank and ventrolateral shoulder to form a broad ventral sinus, which deepens as size increases.

The internal mould (Figs 1D–F, 2A) is smooth save for the constrictions, which are broader and deeper than on the test.

The suture, rather poorly exposed in the present material (see Drushchits 1956: 102, text-fig. 442), includes a large, asymmetrically bifid first lateral saddle (E/L), a smaller, bifid second lateral saddle (L/U_2), separated by a large bifid lateral lobe (L). There are three auxiliary saddles on the suspensive lobe (U_3), the first large and subtrifid, whilst there is a long first, and an incipient second saddle on the internal suture. The septal lobe is horseshoe shaped, and of moderate size (Fig. 1A).

Discussion

The depressed, rectangular whorl section and remarkable constrictions, becoming closely spaced and strongly recurved in adults, together with the deep ventral sinus find an exact match in the large specimens of *Tetragonites heterosulcatus* figured by Drushchits (1960) and Dimitrova (1967), whilst small speci-

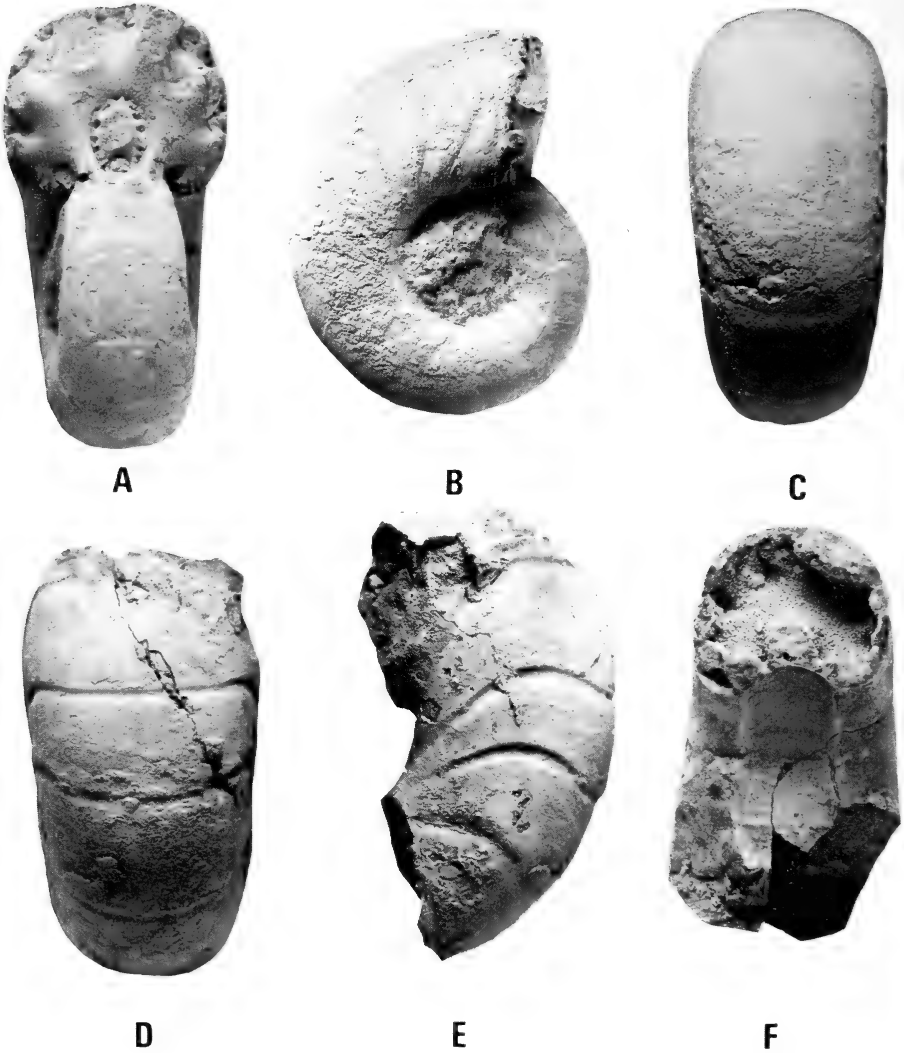

Fig. 1. *Tetragonites? heterosulcatus* Anthula. A–C. BMNH C78827. D–F. BMNH C78828. Both from Bed J of the Mzinene Formation, Albian II–III at locality 171, Mlambongwenya Spruit, northern Zululand. × 1.

mens figured by Drushchits (1956, 1960) link these with Anthula's juvenile holotype. No other *Tetragonites* species shows this combination of characters, whilst the superficially similar *Eogaudryceras* (*Eotetragonites*) such as *E. duvalianum* (d'Orbigny) (e.g. Murphy 1967*a*, pl. 1 (figs 2–3)), *E. umbilicostriatus* Collignon (1963, pl. 248 (fig. 1060)), *E. plurisulcatus* Breistroffer (= *Tetragonites duvali* Anthula (non d'Orbigny) 1899: 99, pl. 7 (fig. 3a–b)), *E. wintunius* (Anderson)

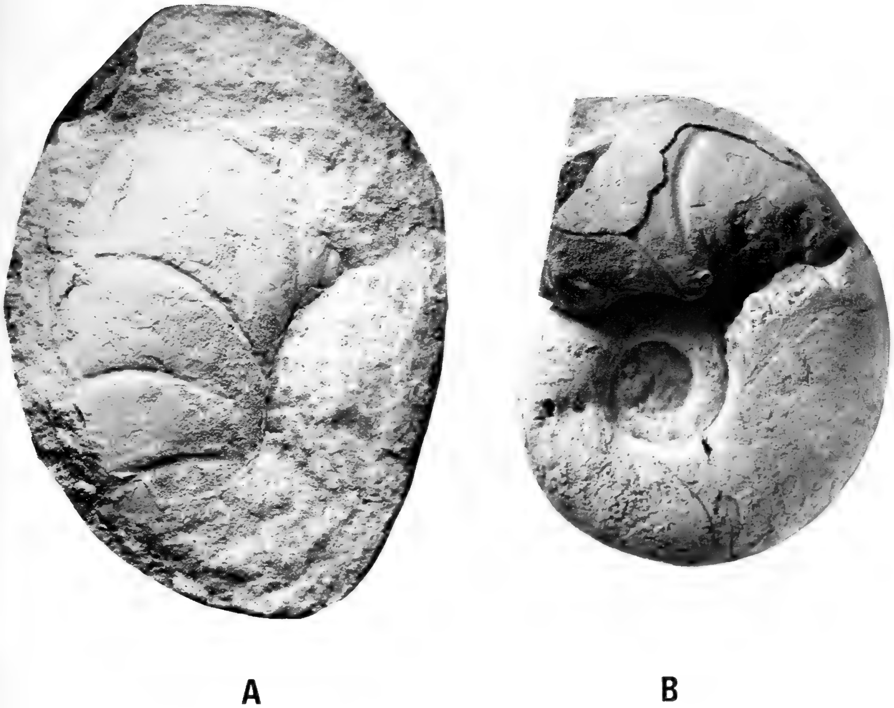

Fig. 2. *Tetragonites? heterosulcatus* Anthula. A. BMNH C78829. B. BMNH 78828. Both from Bed J of the Mzinene Formation, Albian II–III, at locality 171, Mlambongwenya Spruit, northern Zululand. × 1.

(1938, pl. 16 (figs 2–5)). *E. shoupi* Murphy (1967*b*: 22, pl. 3 (figs 7–9)) and *E. jallabertianus* (Pictet) (1848: 302, pl. 4 (fig. 2a–b)) have straight or flexuous constrictions, never develop a strong ventral sinus, and have markedly different relative proportions.

The generic affinity of the species is enigmatic. Murphy (1967*a*, 1967*b*) in the most recent revision of this species placed it in *Tetragonites*. Wiedmann (1973) has subsequently referred the species to *Eotetragonites* because it lacks an umbilical lobe; this divergence reflects the difficulties sometimes encountered in placing forms in the two genera where differing criteria—sutures vs. form of constriction—are used. In consequence the authors have questioned reference of this species to *Tetragonites* until a full review of the *Tetragonites*/*Eotetragonites* plexus is available.

Occurrence

Upper Aptian of Daghestan, the Caucasus and Bulgaria, Aptian of Tunisia, and Lower/Middle Albian of Zululand.

Tetragonites subtimotheanus subtimotheanus Wiedmann, 1962

Figs 3A–C, 4A–F, 5A–H, 6A–G

Ammonites timotheanus Stoliczka, 1865: 146, pl. 73 (figs 3–4, 6) *non* 5.

Lytoceras (*Tetragonites*) *timotheanus* Kossmat, 1895: 133, pl. 17 (figs 11, 13). Collignon, 1928: 18, pl. 1 (fig. 18).

Lytoceras timotheanum Anderson, 1902: pl. 7 (figs 145–148).

Tetragonites timotheanus Crick, 1907: 172, pl. 10 (fig. 15–15a), *non* pl. 13 (fig. 5–5a) (= *Desmoceras latidorsatum* (Michelin)).

Tetragonites aff. *T. timotheanus* Imlay, 1960: 100, pl. 12 (figs 24–28).

Tetragonites subtimotheanus Wiedmann, 1962*a*: 131, 172. Collignon, 1963: 22, pl. 249 (fig. 1071). *Pars.* Murphy, 1967*a*: 62, pl. 5 (figs 11, 13), *non* pl. 6 (figs 5, 8) (= *T. blaisoni* Collignon), text-figs 34–35.

Tetragonites rectangularis alaskaensis Murphy, 1967*a*: 46, pl. 6 (figs 9–10, 14), pl. 7 (figs 2, 9), text-figs 22–23.

?*Tetragonites madagascariensis* Murphy, 1967*a*: 68.

Tetragonites subtimotheanus subtimotheanus Wiedmann, 1973: 592, pl. 1 (fig. 5 ?), pl. 2 (fig. 2), pl. 3 (figs 1–5), pl. 7 (fig. 8 ?), text-fig. 2.

Type

The holotype is the original specimen figured by Kossmat (1895) as pl. 17 (fig. 15), from the lower part of the Utatur Group of southern India. Designated by Wiedmann (1962*a*: 171).

Material

Fourteen specimens from the Mzinene Formation of the Mzinene River and Skoenberg regions: BMNH C78834 from locality 70 (Middle Albian), NMB D367a–b from Bed 7 at locality 51, SAS H207/8/9 from Bed 8 or 9 at locality 51, and BMNH C78835 from Bed 9 or 10 at the same locality (Upper Albian), BMNH C78831 from locality 61 (Albian VI), and C78832–C78833 (Lower–Middle Cenomanian) from locality 62, SAS 689, SAS 1034 and BMNH C18142 are probably from the Lower to Middle Cenomanian of the same locality, whilst a further specimen, SAS 10869, is probably from the Upper Albian of the Mzinene River. UPE 270–271 and BMNH C78836 are from locality 64 (Albian V). A juvenile, BMNH C78837, best referred to as *T.* sp. juv. cf. *subtimotheanus*, comes from locality 106 (Albian V).

Dimensions

	D	*Wb*	*Wh*	*Wb/Wh*	*U*
Holotype (after Kossmat 1895)	35,0	19,0(54)	14,0(40)	1,35	10,0(29)
Indian specimens (after Murphy 1967*a*)					
MHNG 9 Odium, larger specimen	51,7	31,1(60)	21,5(41)	1,45	14,6(28)

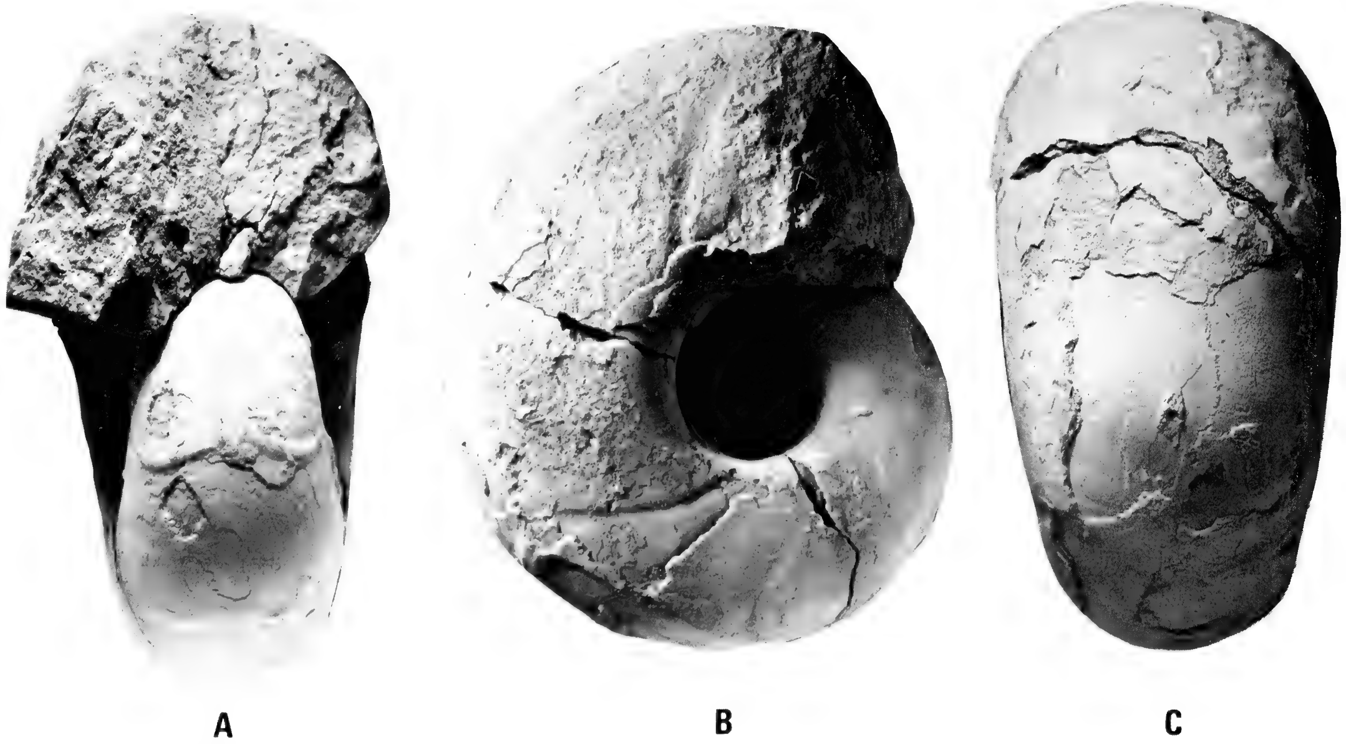

Fig. 3. *Tetragonites subtimotheanus subtimotheanus* Wiedmann. BMNH C78834, from the Mzinene Formation, Albian II, on the farm Izwehelia, north north-east of Hluhluwe, Zululand. × 1.

		D	*Wb*	*Wh*	*Wb/Wh*	*U*
MHNG 9 Odium, smaller specimen 1		32,4	18,5(57)	13,1(40)	1,41	10,1(31)
MHNG 9 Odium, smaller specimen 2		20,3	11,3(56)	8,3(41)	1,36	6,4(32)
Indian specimens (after Kossmat)	a	80,0	45,0(56)	41,0(51)	1,09	16,0(20)
	b	27,0	14,5(54)	10,5(39)	1,38	8,0(30)
BMNH C18142		24,1	13,5(±56)	10,4(43)	1,29	7,0(29)
BMNH C78832		—	18,8(—)	14,2(—)	1,32	—
BMNH C78833		—	13,2(—)	10,1(—)	1,30	—
BMNH C78834	at	50,5	23,7(47)	23,1(46)	1,02	13,9(27)
	at	68,5	38,5(56)	32,8(48)	1,17	19,5(28)
	at	84,0	45,2(54)	37,5(44)	1,20	21,5(25)
SAS A1034		29,4	15,5(53)	12,2(41)	1,27	9,2(31)
SAS A689		19,5	9,9(51)	7,2(37)	1,37	6,2(31,7)
SAS 1869		64,3	36,2(56)	27,3(42)	1,32	15,1(23)
UPE 271		47,5	26,0(55)	22,5(47)	1,15	10,0(21)

Description

The coiling is involute, over two-thirds of the previous whorl being covered. The whorls are trapezoidal, very depressed when young (whorl breadth to whorl height ratio is up to 1,37), becoming somewhat rounded and less depressed when adult (breadth : height ratios of 1,2 to 1,09) and expanding fairly slowly. The greatest breadth is at the umbilical shoulder. The umbilicus is deep, and of moderate size, 28–32 per cent of diameter in the middle growth stages, but becoming proportionally smaller—25 per cent of diameter or less—in larger specimens. The umbilical wall is flat and subvertical, the umbilical shoulder abruptly rounded. The flanks are distinctly flattened and convergent, the ventrolateral shoulder abruptly rounded, and the venter broad and flattened.

The shell surface is finely striate. These striae pass straight across the umbilical wall, running normal to the umbilical seam. They sweep forwards across the umbilical shoulder, and are strongly prorsiradiate over the flank and markedly concave. They flex backwards over the ventrolateral shoulder and form a pronounced sinus over the siphonal area. As size increases, the flexure of the striae increases and they become very concave on both flanks and venter.

There are five or six collar-like ribs and associated constrictions per whorl in smaller specimens; adults bear seven to eight, with some crowding on the body chamber. Collars are faint on the flanks, but strengthen considerably on the shoulder and venter. They are rounded, with a gentle adapical and steep adapertural slope. The constrictions parallel growth striae; they arise at the umbilical seam, are deep across umbilical and ventrolateral shoulders, but relatively weak on flank and venter.

The internal mould is smooth, save for the constrictions, which are far more prominent than on the test. They arise at the umbilical seam, pass straight up the umbilical wall and forwards across the umbilical shoulder, where they are strongly marked. They are concave and strongly prorsiradiate on the flanks and

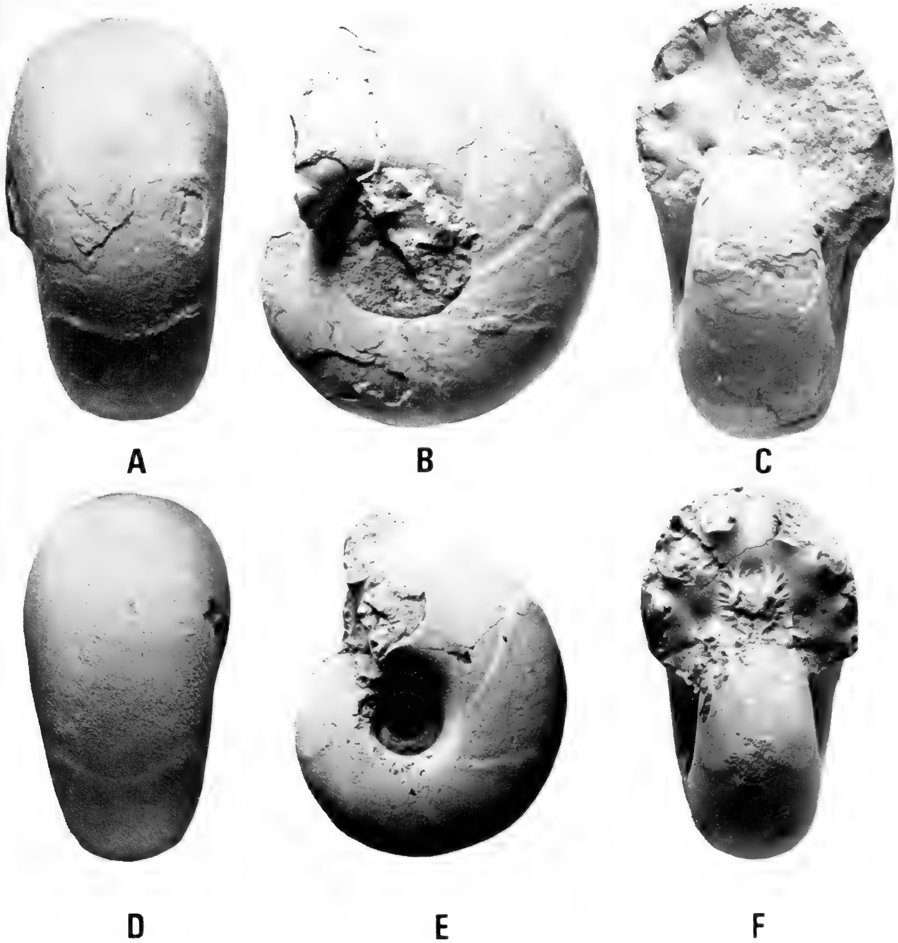

Fig. 4. *Tetragonites subtimotheanus subtimotheanus* Wiedmann. A–C. BMNH C78834, from the Mzinene Formation, Albian II, on the farm Izwehelia, north north-east of Hluhluwe, Zululand. D–F. BMNH C78836, from bed 4 of the Mzinene Formation, Albian V, at locality 71 on the southern tributary of the Munywana Creek, Zululand. This specimen shows a well-preserved septal lobe. × 1.

flex backwards over the shoulder with a striking ventral sinus. The constrictions become broader and more strongly flexed as size increases.

The adult aperture shows features very similar to the collars associated with constrictions, being marked by a thickened lip.

None of the present specimens shows the external suture, but the septal faces

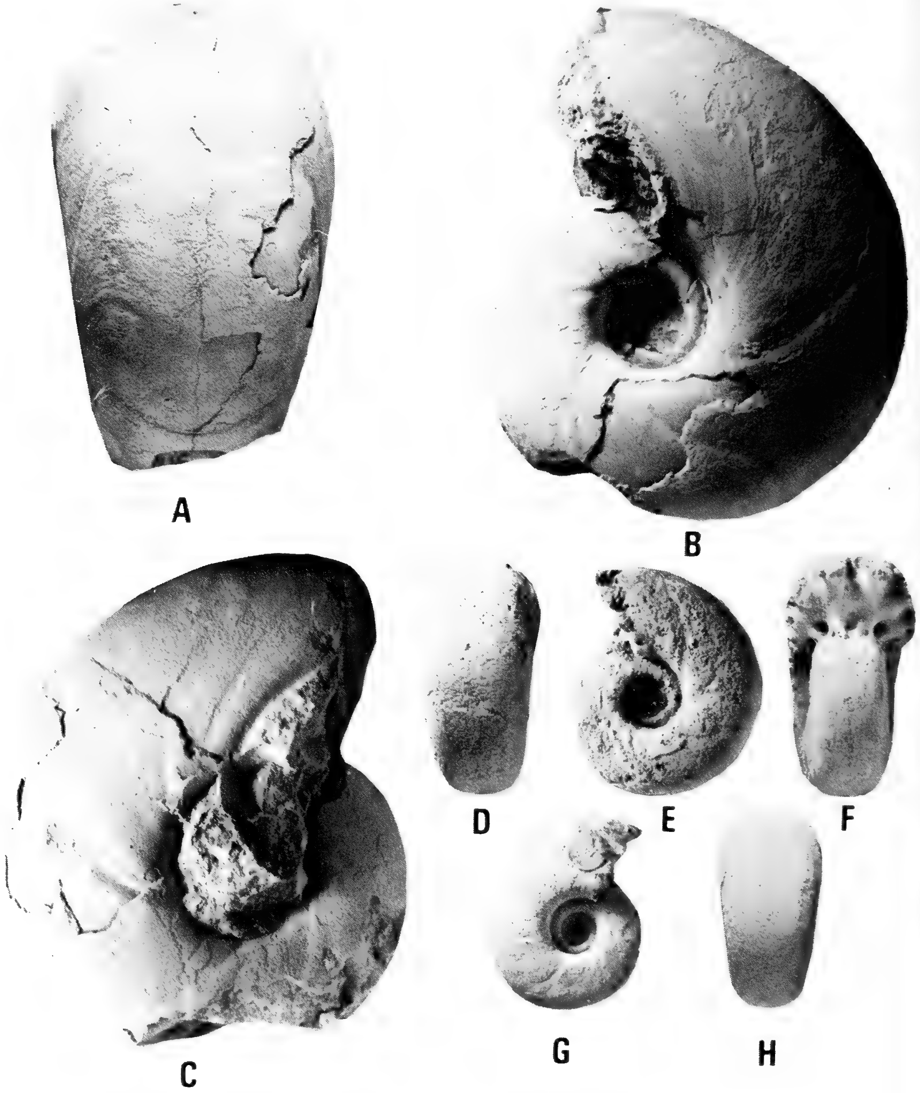

Fig. 5. *Tetragonites subtimotheanus subtimotheanus* Wiedmann. A–C. SAS A10869, from the Upper Albian Mzinene Formation on the Mzinene River, Zululand. D–F. SAS A1034. G–H. BMNH C18142 figured by Crick (1907, pl. 10 (fig. 15–15a)). All from the Lower or Middle Cenomanian Mzinene Formation, Skoenberg, on the Mzinene River, Zululand. × 1.

of a number of specimens show two large internal saddles on either side of the dorsal lobe and a prominent septal lobe (Fig. 4F). Some specimens, including that figured by Crick (1907, pl. 10 (fig. 15–15a)) show, in addition, a tiny third internal saddle.

Discussion

A series of *Tetragonites* ranging from Middle Albian to Middle Cenomanian are linked together by their involute coiling, depressed trapezoidal whorls and markedly flexuous constrictions, collar ribs and growth striae. Although variable in their relative proportions and the degree of incision and flexure of constrictions, reference to a single species seems acceptable. The specimens match closely with *Tetragonites subtimotheanus subtimotheanus* as figured by Stoliczka (1865, pl. 73 (figs 3–3a, 4–4a)), Kossmat (1895, pl. 7 (fig. 13–13a)) and Wiedmann (1973: 592, pl. 1 (fig. 5?), pl. 2 (fig. 2), pl. 3 (figs 1–5), pl. 7 (fig. 8?)). The latter author (Wiedmann 1973: 594) discusses fully how *T. subtimotheanus subtimotheanus* differs from related forms. *T. timotheanus* (Pictet 1848: 295, pl. 2 (fig. 6), pl. 3 (fig. 1)) has a similar juvenile shell, remaining evolute throughout, and loses its constrictions early in ontogeny. *Tetragonites rectangularis* Wiedmann (1962*a*: 178, pl. 14 (fig. 3), text-fig. 39) has a broad, rectangular whorl section at first, losing its distinct ventro-lateral shoulders at a diameter of around 30 mm, whilst the constrictions are straighter, less crowded and decline earlier. *Tetragonites kitchini* Krenkel (1910: 226, pl. 22 (fig. 8)) has a subrectangular whorl section

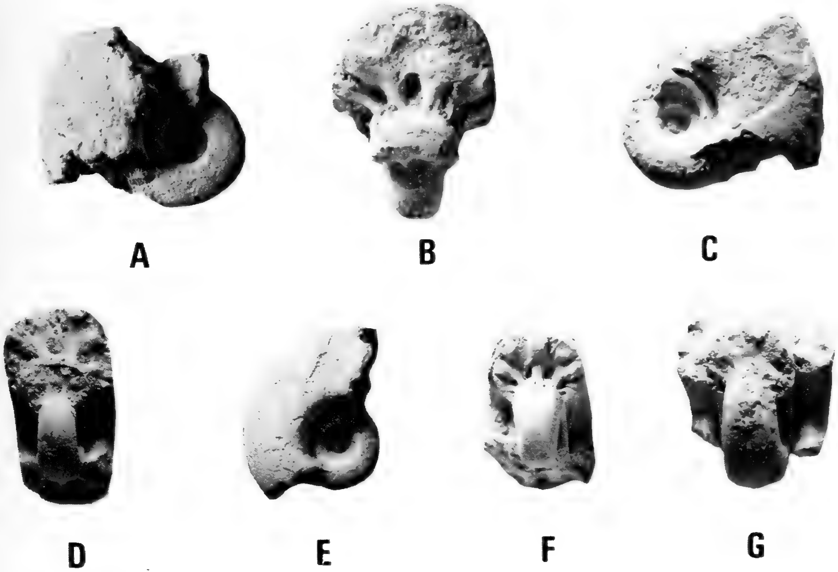

Fig. 6. *Tetragonites subtimotheanus subtimotheanus* Wiedmann. A–C, G. BMNH C78832. D–F. BMNH C78833. Both from the Lower or Middle Cenomanian Mzinene Formation, Skoenberg, on the Mzinene River, Zululand. × 1.

which persists to greater diameters, and generally five constrictions per whorl.

Tetragonites subtimotheanus subspecies *maclearni* Wiedmann (1973: 595, pl. 4 (fig. 1), pl. 5 (figs 1–3), text-fig. 3) has been distinguished from the typical form on the basis of the development of an oval, rather than broadly rounded whorl section in adults (compare Wiedmann 1973, text-figs 2a–e, 3a–b).

Occurrence

This species is known from the upper Lower Albian to Lower Cenomanian of the Queen Charlotte Islands, British Columbia and the Chitina Valley, Alaska, the Upper Albian of Oregon, the Upper Albian and Lower Cenomanian of Madagascar and southern India, and the Middle Albian to Lower (and Middle ?) Cenomanian of Zululand.

Tetragonites superstes Van Hoepen, 1921

Figs 7A–D, H–J, 8, 12A–C

Tetragonites superstes Van Hoepen, 1921: 10, pl. 2 (figs 17–20), text-fig. 6. Spath, 1922: 119, pl. 6 (fig. 6).
Tetragonites cf. *epigonum* Spath, 1921*b*: 42.
Epigoniceras superstes Collignon, 1956: 87, pl. 11 (fig. 3a–b); 1969: 14, pl. 517 (fig. 2034).

Type

The holotype is TM 564, the original of Van Hoepen (1921, pl. 2 (figs 17–18)) from the Umzamba Formation (Late Santonian to Early Campanian) at locality 1, the mouth of the Umzamba River, Transkei (Pondoland).

Material

Seven specimens, TM 525, TM 564–566, BMNH C19416, SAM–K7029, SAM–K7096, all from the Umzamba Formation (Late Santonian to Early Campanian), locality 1, at the mouth of the Umzamba River, Transkei (Pondoland).

Dimensions

	D	*Wb*	*Wh*	*Wb/Wh*	*U*
Holotype TM 564	40,0	18,2(45)	17,3(43)	1,05	10,4(26)
Paratype TM 566	32,4	15,5(48)	14,2(44)	1,09	8,3(26)
From Collignon 1956: 87					
MNHP 2098	44,0	21,0(48)	19,0(43)	1,1	13,0(30)
MNHP 2099	44,0	21,0(48)	18,0(41)	1,1	13,0(30)
MNHP 2100	52,0	22,0(42)	22,0(42)	1,0	14,0(27)

Description

The shell is small and involute with a moderately high expansion rate. The whorl section is depressed (whorl breadth : height ratio 1,05 to 1,15) with the greatest breadth just below mid-flank. The umbilicus is about 26 per cent of the diameter, rather deep, with a subvertical wall of moderate height. The umbilical shoulder is abruptly rounded, the flanks gently rounded, merging with broadly rounded shoulders and venter. The whorl section is thus between subrectangular and elliptical. The surface of the test bears very fine prorsiradiate growth striae, whilst the internal mould is smooth. Some individuals show faint spiral ridges, one over the siphonal area and a pair on each shoulder (Figs 7D, H, 12C).

Constrictions are faint on the mould, and virtually invisible when the shell is preserved. They appear to be absent on juveniles, but up to four per half-whorl are present during the later growth stages, as in TM 566. The mature aperture, present on a number of specimens (Fig. 7A, C) is also constricted. These apertural constrictions are deep and quite wide, originating at the umbilical seam. They pass normally across the inner part of the umbilical wall and are strongly prorsiradiate across the flanks, flexing backwards across the ventrolateral shoulders and passing across the venter with a shallow, concave ventral sulcus.

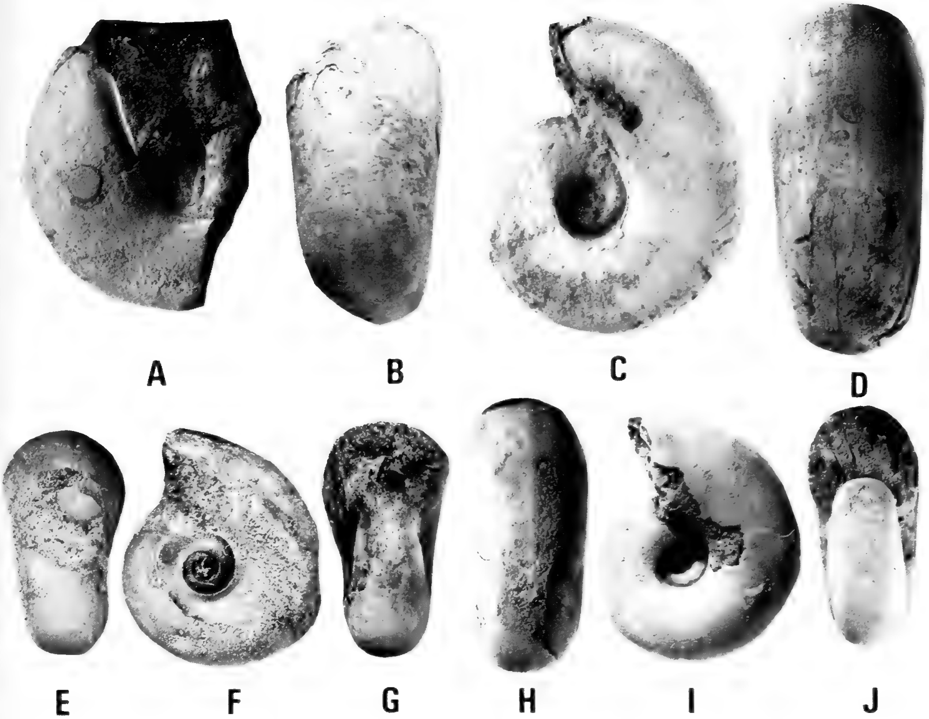

Fig. 7. A–D, H–J. *Tetragonites superstes* Van Hoepen. A–B. BMNH C19416 (original of Spath 1922, pl. 6 (fig. 6)). C–D. Holotype, TM 564. H–J. TM 566, a paratype. E–G. *Tetragonites* cf. *epigonus* Kossmat. An unregistered specimen in the collections of the Durban Museum. All specimens are from the Umzamba Formation, of late Santonian to early Campanian age, at locality 1, the mouth of the Umzamba River, Pondoland. × 1.

The suture line (Fig. 8) has a large, asymmetric trifid first lateral saddle (E/L), a smaller trifid second lateral saddle (L/U_2), and a suspensive lobe with a large trifid first auxiliary saddle. The first lateral lobe (L) is large and irregularly subdivided. The first of the four auxiliary lobes is trifid.

Discussion

Tetragonites superstes most closely resembles *Tetragonites popetensis* Yabe (1903: 48, pl. 7 (figs 4a–b, 6)), a Campanian to Maastrichtian species known from Japan and California. In Yabe's species the position of the constrictions is rather clearly marked on the shell surface by rounded ribs,which are markedly flexed. The shell is also more evolute ($U = 31\%$ at a diameter of 34 mm in the type).

Differing proportions and number and style of constrictions readily separate *Tetragonites superstes* from contemporary species such as *Tetragonites glabrus* Jimbo and its variety *problematica* Matsumoto (1942: 672, figs 1–1b, 2a–2b), *Tetragonites garuda* (Forbes) (1846: 102, pl. 7 (fig. 1a–c)), *Tetragonites mitraikyense* Collignon (1956: 86, pl. 11 (fig. 2–2b)), *Tetragonites beantalyensis* Collignon (1956: 83, pl. 10 (fig. 1–1b)) and the various species revised by Henderson (1970).

Occurrence

All present material comes from the Umzamba Formation of Transkei (Pondoland), and cannot be dated more accurately than Late Santonian to Early Campanian. The species is also known in Madagascar where it occurs from Lower to Middle Campanian.

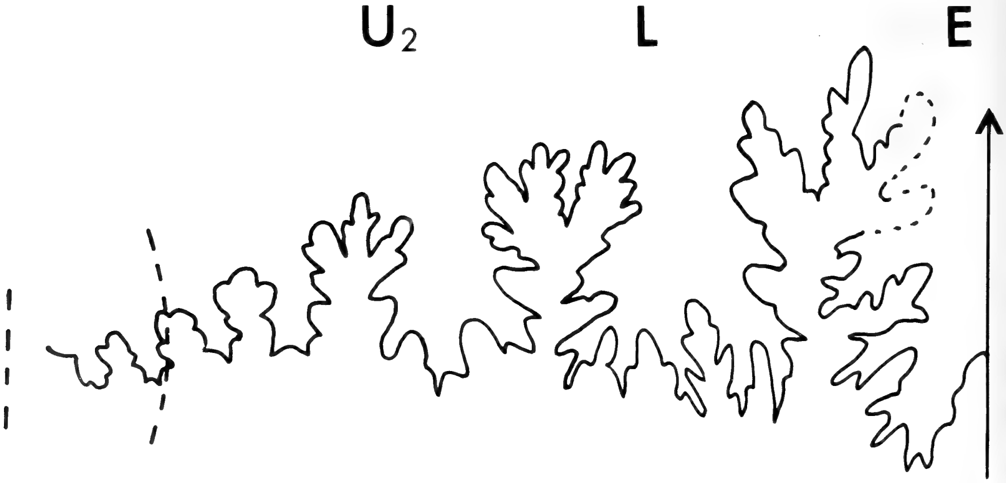

Fig. 8. External suture of *Tetragonites superstes* Van Hoepen. TM 564. × 10.

Tetragonites cf. *epigonus* Kossmat, 1895

Figs 7E–G, 9A–C

Compare:

Ammonites timotheanus Stoliczka, 1865: 146, pl. 73 (fig. 5 only).

?*Desmoceras pyrenaicum* De Grossouvre, 1894: 168, pl. 25 (fig. 2), *non* pl. 37 (fig. 9), text-fig. 73.

Lytoceras (*Tetragonites*) *epigonus* Kossmat, 1895: 135, pl. 17 (figs 4a–c, 5a–b, 10). Kilian & Reboul, 1909: 14.

?*Tetragonites timotheanus* Whiteaves, 1903: 329.

Tetragonites cf. *epigonus* Yabe, 1903: 49, pl. 7 (fig. 3).

non *Lytoceras* (*Tetragonites*) *epigonum* Boule, Lemoine & Thévenin, 1906: 13, pl. 3 (fig. 1–1a). This specimen is an Albian desmoceratid. Marshall, 1926: 149, pl. 21 (fig. 10), pl. 29 (figs 6–7) = *Tetragonites marshalli* Collignon. Anderson, 1958: 187, pl. 65 (figs 4–5), pl. 67 (fig. 3–3a) = *Tetragonites popetensis* Yabe.

Lytoceras (*Tetragonites*) *epigonum* Pervinquière, 1907: 76, pl. 3 (figs 27–28), text-figs 15–16. Basse, 1928: 461, pl. 30 (figs 1–3). Collignon, 1931: 14, pl. 2 (figs 5–7), pl. 3 (fig. 4).

Tetragonites epigonus Paulcke, 1906: 174.

?*Tetragonites* sp. indet. Spath, 1921*b*: 42, pl. 7 (fig. 3).

? *Epigoniceras epigonum* Spath, 1925: 29, pl. 1 (fig. 2a–b).

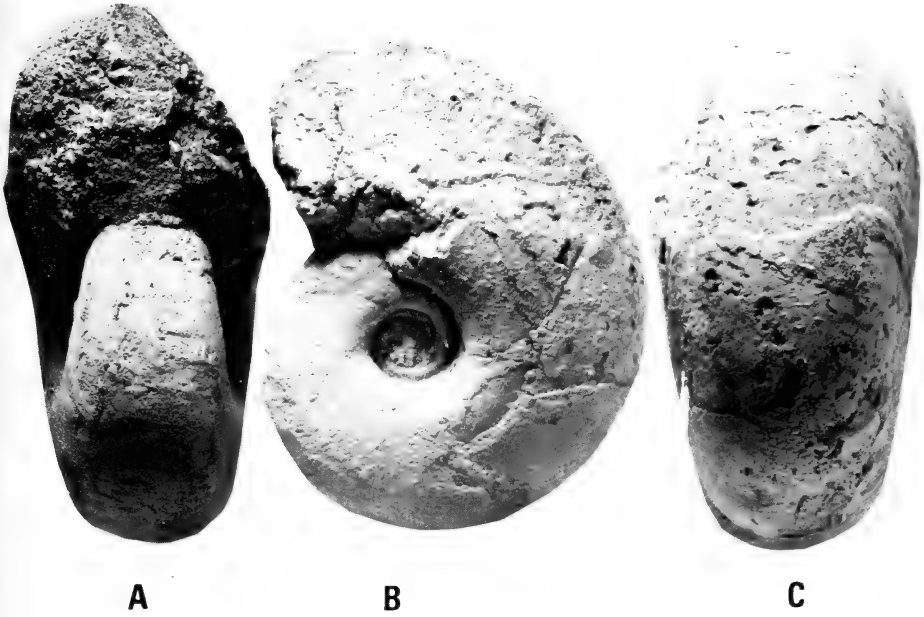

Fig. 9. *Tetragonites* cf. *epigonus* Kossmat. BMNH C78838, from the St Lucia Formation, Campanian IV–V, at locality 73, on the lower reaches of the Mzinene River, Zululand. × 1.

? Lytoceras (*Tetragonites*) aff. *epigonus* Basse, 1939: 45.
Epigoniceras epigonum Matsumoto, 1942: 671. Usher, 1952: 55, pl. 2 (figs 6–7), pl. 3 (fig. 1), pl. 31 (fig. 13). Collignon, 1956: 85; 1965*a*: 8, pl. 417 (fig. 1723); 1966: 3, pl. 456 (fig. 1855).
Tetragonites jurianus angolanus Haas, 1952: 12–15, figs 21, 23–25 only.
Tetragonites cf. *epigonus* Howarth, 1958: 9, pl. 1 (fig. 12a–b).
Tetragonites epigonus Matsumoto, 1959: 153, text-fig. 75.

Type

Lectotype (herein designated) is the original of the larger of Kossmat's (1895, pl. 17 (fig. 4a–c)) figured specimens.

Material

Two specimens; a dubious juvenile in the collections of the Durban Museum, figured by Spath (1921*b*, pl. 7 (fig. 3)) from the Umzamba Formation of Late Santonian or Early Campanian age, locality 1, the mouth of the Umzamba River, Transkei (Pondoland), and a further specimen, BMNH C78838 from the St Lucia Formation at locality 73 on the lower Mzinene River (Coniacian IV–V).

Dimensions

	D	*Wb*	*Wh*	*Wb*/*Wh*	*U*
BMNH C78838. Maximum diameter is 71 mm. Proportions at:					
	65,0	—	31,3(48)	—	14,5(22)
	51,5	28,5(55)	26,0(50)	1,09	12,0(23)
From Kossmat (1895: 135)					
	59,0	27,0(46)	26,0(44)	1,04	15,0(25)
	23,0	11,0(44)	10,0(43)	1,1	7,0(30)

Description

The coiling is involute, the whorls expanding at a moderate rate. The whorl section is slightly depressed, with the greatest breadth close to the umbilical shoulder. The umbilicus is small (22% of the diameter) and relatively deep, with a high, subvertical wall. The umbilical shoulder is abruptly rounded whilst the sides are somewhat flattened and convergent, the ventro-lateral shoulders distinct and the rather wide venter broadly rounded.

The shell surface is corroded, and no trace of ornament remains. Traces of seven constrictions are, however, visible on the outer whorl, each associated with a low, rounded rib. The constrictions arise at the umbilical seam, pass straight up the umbilical wall, sweep forwards across the umbilical shoulder and are markedly prorsiradiate and slightly concave across the flanks; they flex distinctly backwards over the ventro-lateral shoulders, and there is a broad, shallow ventral sinus. The sutures are not exposed.

Discussion

The juvenile specimen noted by Spath (1921*b*; 1922, pl. 4 (fig. 1a–c)) is difficult to place with certainty, but the lack of ornament, relative proportions, umbilical wall and flank shape all match closely with Kossmat's (1895, pl. 17 (fig. 5a–b)) smaller specimen. The authors' other specimen, although poorly preserved, has proportions, whorl section and constrictions, all of which suggest reference to Kossmat's species.

Occurrence

Tetragonites epigonus is a long-ranging form known from the Turonian to the Campanian. Its geographic distribution includes Antarctica, Angola, Madagascar, Japan, southern India, British Columbia, south Patagonia, north Africa and southern France. In South Africa the Pondoland occurrence can be dated no more firmly than Late Santonian to Early Campanian. The Zululand example is firmly dated as Coniacian IV–V.

Genus *Saghalinites* Wright & Matsumoto, 1954

Type species

Ammonites cala (Forbes, 1846: 104, pl. 8 (fig. 4a–c)) by original designation of Wright & Matsumoto (1954: 110).

Diagnosis

Very evolute tetragonitids with a low expansion rate, the whorls being slightly depressed. The whorl section is typically rounded when young, becoming distinctly octagonal during later growth stages in most species. The shell surface is smooth, or bears only growth striae. Constrictions are consistently present, and may be weak to strong, straight or sinuous. The suture is relatively simple, with trifid major saddles, and a retracted suspensive lobe.

Discussion

The name *Saghalinites* was introduced by Shimizu in 1934 as a *nomen nudum*; validation extends from the work of Wright & Matsumoto in 1954. Originally proposed as a subgenus of *Epigoniceras* Spath, 1925, the work of Howarth (1958), Matsumoto (1959) and Wiedmann (1962*a*, 1962*b*, 1973) suggests that *Epigoniceras* does not bear separation from *Tetragonites sensu stricto*, as noted elsewhere (p. 151). Howarth and Matsumoto have treated *Saghalinites* as a subgenus of *Tetragonites*, whilst Birkelund (1965) and Wiedmann (1962*a*), amongst others, have given it full generic status. Wiedmann (1973: 589) has subsequently suggested that *Saghalinites* is no more than a synonym of *Tetragonites*. In the authors' views, however, the features of the type species and other well-known Santonian to Maastrichtian species referred to the genus indicate a distinct monophyletic offshoot from contemporaneous *Tetragonites* which merits generic separation; the group appears as distinctive as the bulk of the genera of Tetragonitaceae.

Saghalinites is readily separable from *Pseudophyllites* Kossmat, 1895, in that that genus is inflated, very involute, and typically has a rounded whorl, higher than wide, and is ornamented by longitudinal and transverse striae, whilst the suture line is highly subdivided and there are no constrictions.

Tetragonites Kossmat, 1895, is also typically more inflated, with a higher expansion rate, and more involute coiling.

The origin of *Saghalinites* clearly lies in *Tetragonites*, from which it evolved in the Late Santonian (or possibly the Coniacian, according to Collignon (1956: 82)).

The following species and varieties have been referred to the genus:

1. *Saghalinites cala* (Forbes) (1846: 104, pl. 8 (fig. 4a–c)). Campanian to Maastrichtian.
2. *Saghalinites nuperus* (Van Hoepen) (1921: 13, text-fig. 8, pl. 3 (figs 3–4)). Santonian to Lower Campanian.
3. *Saghalinites zeugitanus* (Pervinquière) (= *Tetragonites cala* var. *zeugitana* Pervinquière, 1907: 79, pl. 3 (fig. 3a–b)). ? Santonian.
4. *Saghalinites zelandicus* Shimizu, 1935 (= *Gaudryceras politissimum* Marshall (*non* Kossmat), 1926: 143, pl. 20 (fig. 3), pl. 28 (figs 1–2), but is, in fact, a crushed *Anagaudryceras particostatum* (Marshall); fide Henderson 1970).
5. *Saghalinites kingianus* (Kossmat, 1895) (= *Ammonites cala* Stoliczka (*non* Forbes), 1865: 153, (*pars*) pl. 75 (fig. 4)). ? Santonian to Campanian.
6. *Saghalinites kingianus* (Kossmat) var. *involutor* Paulcke (1906: 174, pl. 17 (figs 3–4)). Campanian.
7. *Saghalinites wrighti* Birkelund (1965: 30, pl. 1 (fig. 5), pl. 2 (figs 1a–c, 5a–c), pl. 3 (fig. 1), text-figs 14–25). Maastrichtian.

Occurrence

Saghalinites first appears in the Santonian and ranges to the Lower Maastrichtian. Species have a wide geographic distribution; there are records from Antarctica, south Patagonia, Zululand, Madagascar, South Africa, Japan, Sakhalin, southern India and Greenland.

Saghalinites cala (Forbes, 1846)

Figs 10A–B, 11A–B, 12D–G, 13A–B, E–K, ? C–D, 14A–F, 15A–F

Ammonites cala Forbes, 1846: 104, pl. 8 (fig. 4a–c). *Non* Kossmat, 1895: 153, pl. 75 (fig. 4) =*Saghalinites kingianus* (Kossmat).
Lytoceras (*Tetragonites*) *cala* Kossmat, 1895: 136, pl. 17 (fig. 12a–d).
non *Tetragonites* cf. *cala* Anderson, 1902: 84. Yabe, 1915: 16, pl. 1 (fig. 7), pl. 3 (fig. 2) =*Saghalinites nuperus* Van Hoepen.
?*Tetragonites* aff. *cala* Woods, 1906: 335, pl. 41 (fig. 7a–c).
Tetragonites cala (Forbes) var. *zeugitana* Pervinquière, 1907: 79, pl. 3 (fig. 30), text-fig. 18.
non *Tetragonites cala* Kilian, 1922: 176.
Tetragonites cala Shimizu, 1935: 181.
Saghalinites cala Spath, 1953: 9. Collignon, 1956: 99.
Tetragonites (*Saghalinites*) *cala* Howarth, 1958: 10, pl. 1 (fig. 11a–b).

Type

The lectotype is Forbes's original figured specimen, BMNH C51057, from the Valudayur Beds (Campanian–Maastrichtian) of Pondicherry, southern India.

Material

The authors have numerous specimens, as follows: SAS H163/E1, E2 and E6, H163/3, H163B/2, 4 and 5, H163C/2 and 12, H163G/1, all from locality 20 south of Lake Mfuthululu, east-south-east of Mtubatuba (Maastrichtian I–II); BMNH C78840–43 from locality 113 at the south-eastern corner of the Nibela Peninsula, Lake St Lucia (Campanian IV); SAS Z2267–2267e from this locality and to the area to the immediate west; SAS H104/1 from locality 117 at the north-eastern tip of the southern Peninsula (Campanian IV); SAS Z2242 and 2248a–b, H119/11, H115/10 and 11 from locality 119; BMNH C78862 and C78863 from locality 120; BMNH C78861 from locality 121, The Coves, on the eastern shores of the southern Peninsula (Campanian III–IV); BMNH C18857–60 from locality 124 north of Fanies Island Rest Camp on the eastern shores of the southern Peninsula (Campanian III–IV); BMNH C78856 from locality 126, south of the Camp (Maastrichtian II); BMNH C78853–C78855 from locality

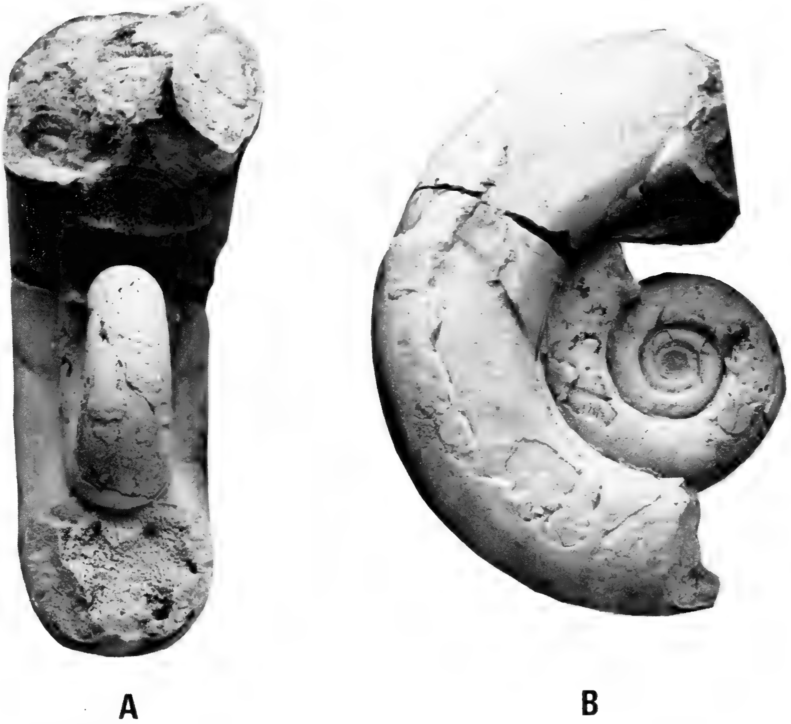

Fig. 10. *Saghalinites cala* (Forbes). BMNH C51058, the original of Kossmat (1895, pl. 17 (fig. 12a–d)), from the Valudayur Beds (Campanian–Maastrichtian) of Pondicherry, southern India. × 1.

132; BMNH C78844 and SAS specimens A1252, 2087, H60F/6, 60H/6 and 16217 from locality 133; BMNH C78845–C78852, and SAS specimens H63/2, 10, 13–14, 22–25, H61/1, 2, 5, 7, 9, 12, 18, H64/1–4, 6, 9, and Z2210a–k from locality 134 in the area of Charters Creek Rest Camp, Lake St Lucia (Maastrichtian I); and SAS H66/1 from locality 135, Makakatana Bay, Lake St Lucia (Maastrichtian I). There is a single juvenile specimen, SAM–4808, from the Umzamba Formation at locality 1, the mouth of the Umzamba River, Transkei (Pondoland) (Late Santonian to early Campanian) which may belong here.

Dimensions

	D	*Wb*	*Wh*	*Wb/Wh*	*U*
Lectotype					
BMNH C51057	32,3	13,7(42)	9,9(31)	1,38	14,4(45)
BMNH C51058	78,8	30 (38)	23,9(30)	1,25	37,4(47)
SAS H60/12	66,8	—	20,5(30)	—	31,2(46)

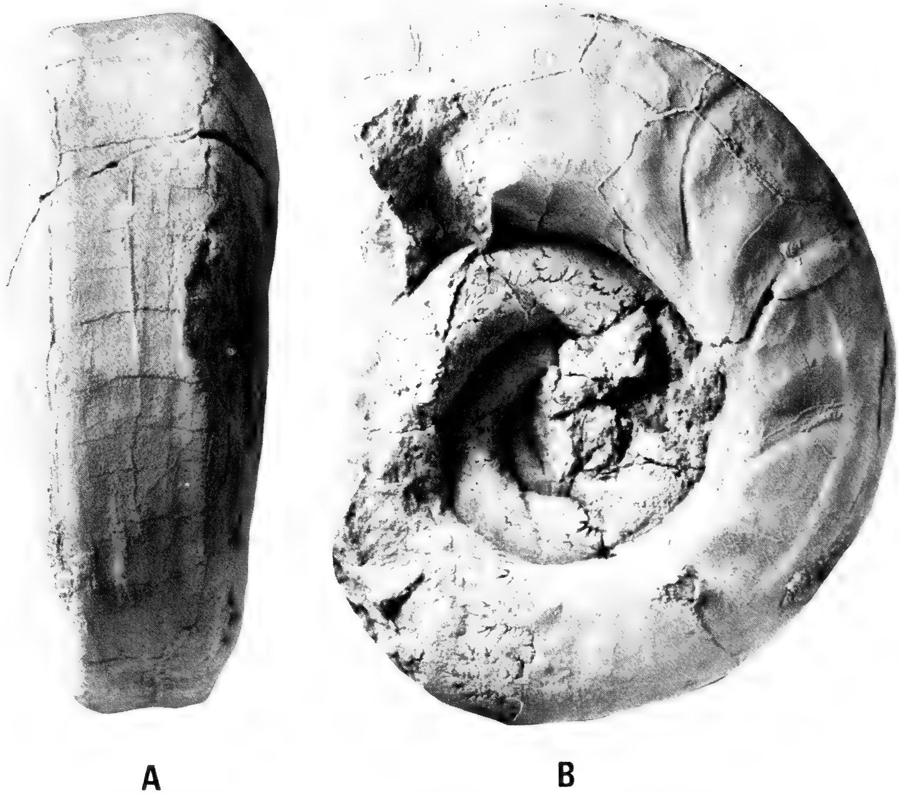

Fig. 11. *Saghalinites cala* (Forbes). SAS H163b/2, from the St Lucia Formation, Maastrichtian I–II, at locality 20, south of lake Mfuthululu, east south-east of Mtubatuba, Zululand. The specimen shows coarse lateral folds associated with constrictions, a distinctly sulcate venter, and spiral ridges on both flank and venter. × 1.

Lectotype		*D*	*Wb*	*Wh*	*Wb/Wh*	*U*
SAS H61/11		76,5	29,2(38)	21,9(28)	1,33	36,1(47)
SAS H163/D		89,0	38,5(43)	28,2(31)	1,36	40,5(45)
BMNH C78855	at	28,2	11,1(39)	9,4(33)	1,18	12,4(44)
	at	63,0	23,3(37)	18,5(29)	1,25	30,0(47)
BMNH C78843		91,8	—	29,7(32)	—	42,0(46)
BMNH C78863		99,5	—	31,8(32)	—	46,4(46)
SAS Z2270k		60,5	21,5(35)	18,5(31)	1,16	28,5(47)
SAS A1214		88,5	31,5(36)	28,0(32)	1,12	43,0(49)

Description

The bulk of the material occurs either as composite or internal moulds.

Juveniles, up to 30 mm diameter (Figs 12E–F, 13A–D, G–K)

The coiling is evolute, slowly expanding, the whorl section depressed and rounded, the whorl breadth : height ratio being around 1,2, the greatest breadth some distance below mid-flank. The umbilicus is broad, 44 per cent of the diameter, shallow, with a low, rounded, undercut wall. The flanks are rounded, and there is a broad, rounded venter. The surface of the mould is smooth, with six prominent, narrow constrictions. The constrictions arise at the umbilical seam, pass straight up the umbilical wall, and straight across the inner flanks in a markedly prorsiradiate direction, flexing gently backwards across the upper flank and shoulder to form a shallow concave sinus over the siphonal area.

Middle growth stages, 30 to 60 mm diameter (Figs 12D, 14A–F)

The coiling remains evolute, but the whorl section becomes more depressed, the whorl breadth : height ratio being up to 1,25 and the whorl section changing from depressed oval to polygonal.

The umbilical wall increases in height, is flat, and inclined outwards, the umbilical shoulder is abruptly rounded, the whorl sides flattened and convergent, the ventrolateral shoulder abruptly rounded, the venter, broadly rounded at first, becomes flattened, and in some cases concave. Constrictions become increasingly flexed, sweeping forwards over the inner flanks, flexing backwards at mid-flank and developing a broad, shallow but distinct ventral sinus. The number of constrictions increases, with up to eight per whorl in some specimens.

Many specimens show a range of structures associated with the siphonal band (Fig. 14A, D), as discussed below.

60 mm Onwards (Figs 11A–B, 12G)

The largest specimens present are still incomplete at 100 mm and are the largest known representatives of the genus. Up to two-thirds of the outer whorl is body chamber in these specimens. The whorl section is polygonal, as in middle growth stages, but there is an increase in the degree of ventral concavity, and many specimens develop a low, but distinct, rounded siphonal ridge and related structures.

Constrictions become stronger, deeper, closer spaced and more markedly flexed on body chambers, and there is a tendency for the lower part of the flank between constrictions to become irregularly swollen (Fig. 11A–B). In other specimens, broad, flexuous folds are present on the flanks, and seem to represent an exaggerated development of this feature. Yet other specimens show low, rounded, spiral ridges on their flanks (Fig. 13E–F).

The few external moulds of the outer shell surface available suggest that it

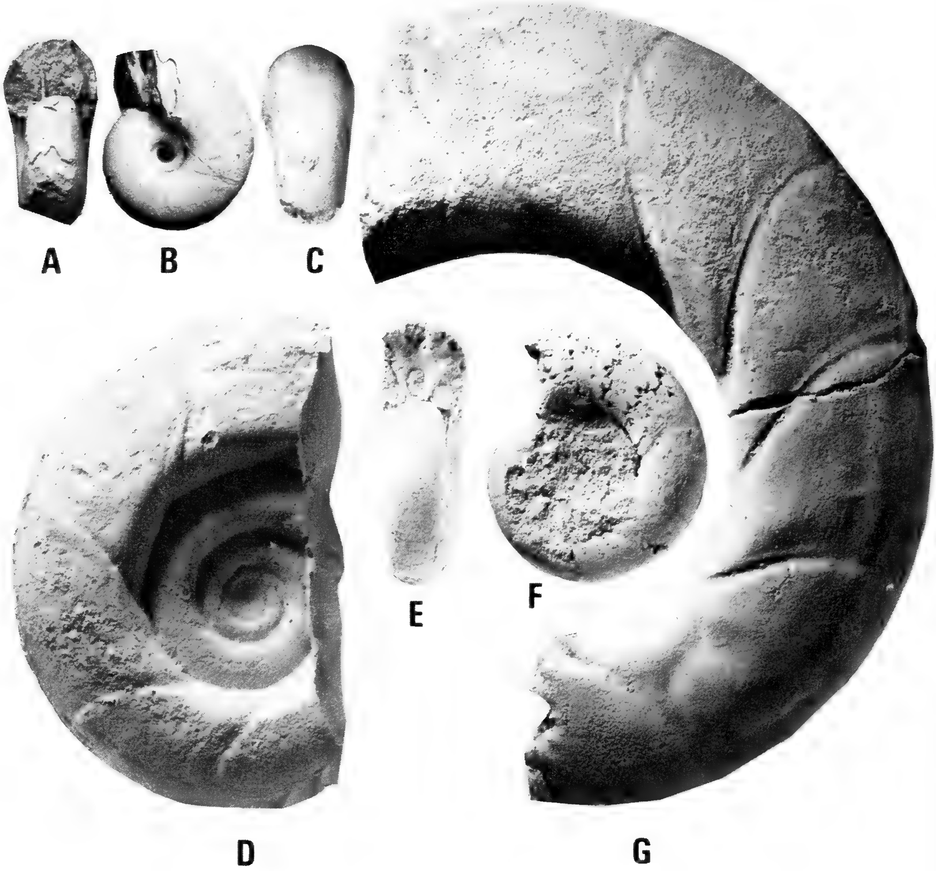

Fig. 12. A–C. *Tetragonites superstes* Van Hoepen. TM 7029, from the late Santonian–early Campanian Umzamba Formation at locality 1, the mouth of the Umzamba River, Pondoland. D–G. *Saghalinites cala* (Forbes). D. A silicone mould taken from BMNH C78841, from the St Lucia Formation, Campanian IV, at the south-eastern corner of the Nibela Peninsula, Lake St Lucia, Zululand. E–F. BMNH C78856, from the St Lucia Formation, Maastrichtian II, at locality 126, south of Fanies Island Rest Camp, on the eastern shores of the southern Peninsula, Lake St Lucia, Zululand. G. BMNH C78863, from the St Lucia Formation, Campanian III–IV, locality 120, The Coves, on the eastern side of the southern Peninsula, Lake St Lucia, Zululand. A–D, G, × 1; E–F, × 2.

bore faint growth striae, parallel to the constrictions, whilst the constrictions are themselves rather less conspicuous on the shell exterior, being associated with a low, collar-like rib (Fig. 12D).

The external suture line (Figs 14A–C, 15) is rather simple, with a large first lateral saddle (E/L), and a smaller second lateral saddle (L/U_2), both of which are irregularly trifid. The suspensive lobe is strongly retracted, the auxiliary lobes and saddles decreasing rapidly in size. The lateral lobe (L) is markedly bifid.

The internal suture has a deep dorsal lobe and a narrower lateral lobe

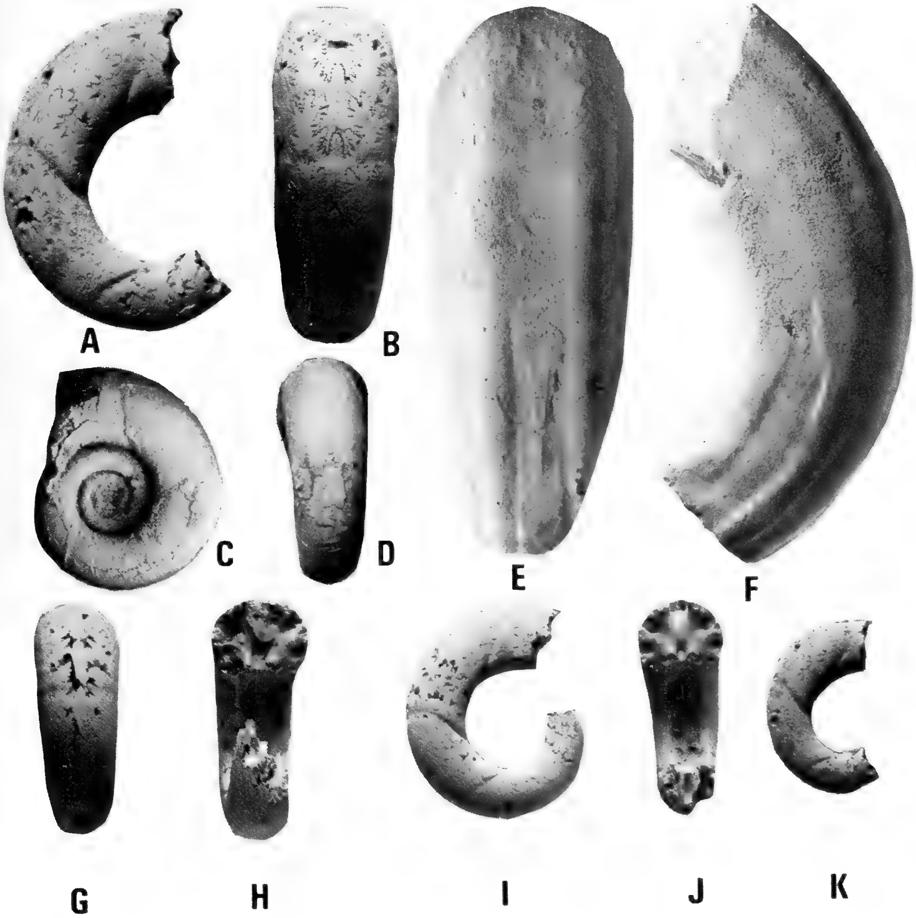

Fig. 13. *Saghalinites cala* (Forbes). A–B, G–K. BMNH C78855, from the St Lucia Formation, Maastrichtian I, at locality 132, near Charter's Creek Rest Camp, Lake St Lucia, Zululand. E–F. BMNH C78851, from the St Lucia Formation, Maastrichtian I, near Charter's Creek Rest Camp, Lake St Lucia, Zululand. The specimen is an internal mould of a body chamber lacking constrictions, and showing lateral and ventral spiral ridges. C–D. SAM–4808, best referred to as *Saghalinites* cf. *cala* (Forbes) ?, from the late Santonian to early Campanian Umzamba Formation at locality 1, the mouth of the Umzamba River, Pondoland. A–B, × 2; C–K, × 1.

extending to about half the depth. The first saddle is tall and narrow, the second much smaller (Fig. 14B, F).

Discussion

The large number of specimens available show very variable adult features, especially the nature and development of constrictions and lateral folds on the body chamber, the degree of concavity of the venter and the extent of the siphonal band. In spite of this, the authors feel confident in referring their specimens to Forbes' species on the basis of the comparable and distinctive ontogenetic changes, the markedly similar polygonal whorl section of adults, distinctly sigmoidal constrictions and overall comparable relative proportions.

Comparable variability in whorl section and venter form has been described in *Saghalinites wrighti* from the Maastrichtian of west Greenland (Birkelund 1965: 30 et seq., especially text-figs 14–20). *S. cala* and *S. wrighti* can, however, be differentiated on the basis of the absence of constrictions on the early whorls of *S. wrighti*, the fewer constrictions on the later whorls, and their straight rather than flexuous course.

S. cala can readily be separated from both *S. nuperus* and the doubtful *S. kingianus* on the basis of its sinuous rather than straight constrictions, and the development of a polygonal whorl section during later growth stages rather than the rounded section retained by these forms.

Pervinquière's *Lytoceras* (*Tetragonites*) *cala* var. *zeugitana* (1907: 79, pl. 3 (fig. 30a–b)) is based on a specimen only 13 mm in diameter and was separated from the typical form on the basis of the more angular, trapezoidal whorl section and more flexuous constrictions. It seems doubtful if it indeed merits separation in view of the great variability as described above, but since it is said to be of Santonian age, it may conceivably be the juvenile of some other species.

As already noted, many of the present specimens show beautifully ventral structures resembling those described by Grandjean (1910: 502–503), Neaverson (1927), Hölder (1955), Vogel (1959: 510–511), Jordan (1968: 28) and Birkelund (1965: 36).

On internal moulds of body chambers (Figs 11A, 13E–F), the chief structure is a low, flat-topped ridge, marked off on either side by a distinct narrow groove and extending from the aperture to the last septum. When intersected by constrictions, the ridge is weakened, but nevertheless continuous across the constriction. It thus appears that this structure corresponds to the presence of a pair of parallel ridges on the shell interior. On the phragmocone during later growth stages (Fig. 14A, D), this ridge is usually subdued, or its site marked by a band corresponding in width to the ventral lobe. The band is bisected by a continuous median groove, and the surface is covered by fine, longitudinal striae which converge slightly when traced in an apical direction from one suture to the next. In some cases, concave transverse striae are present in the area enclosed by the siphonal lobe, giving rise to a distinctive reticulate pattern (*Schleppstreifen* of Hölder 1955: 374), whilst the ventral band in some juveniles is ornamented by a curious chevron-like striation. The interpretation of these structures is far from clear; Jordan (1968) suggested that the ventral ridge represents the trace of a muscle system controlling a pre-septal gas and fluid-filled space, but it is difficult to reconcile this with the extension of the band throughout the length of the body chamber. The striations of the siphonal band on the phragmocone are typically interpreted as the site of muscle or ligament insertion associated with

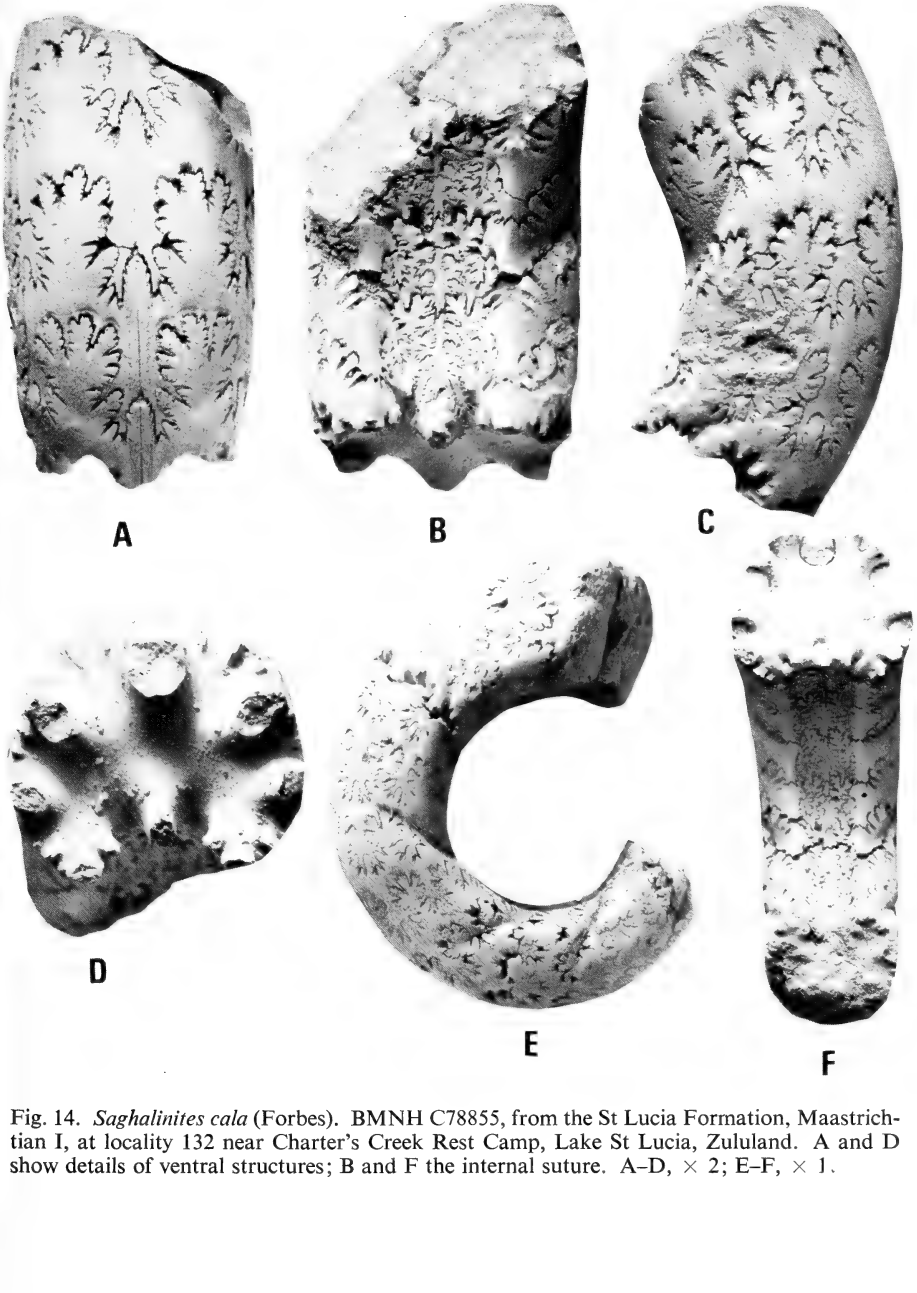

Fig. 14. *Saghalinites cala* (Forbes). BMNH C78855, from the St Lucia Formation, Maastrichtian I, at locality 132 near Charter's Creek Rest Camp, Lake St Lucia, Zululand. A and D show details of ventral structures; B and F the internal suture. A–D, × 2; E–F, × 1.

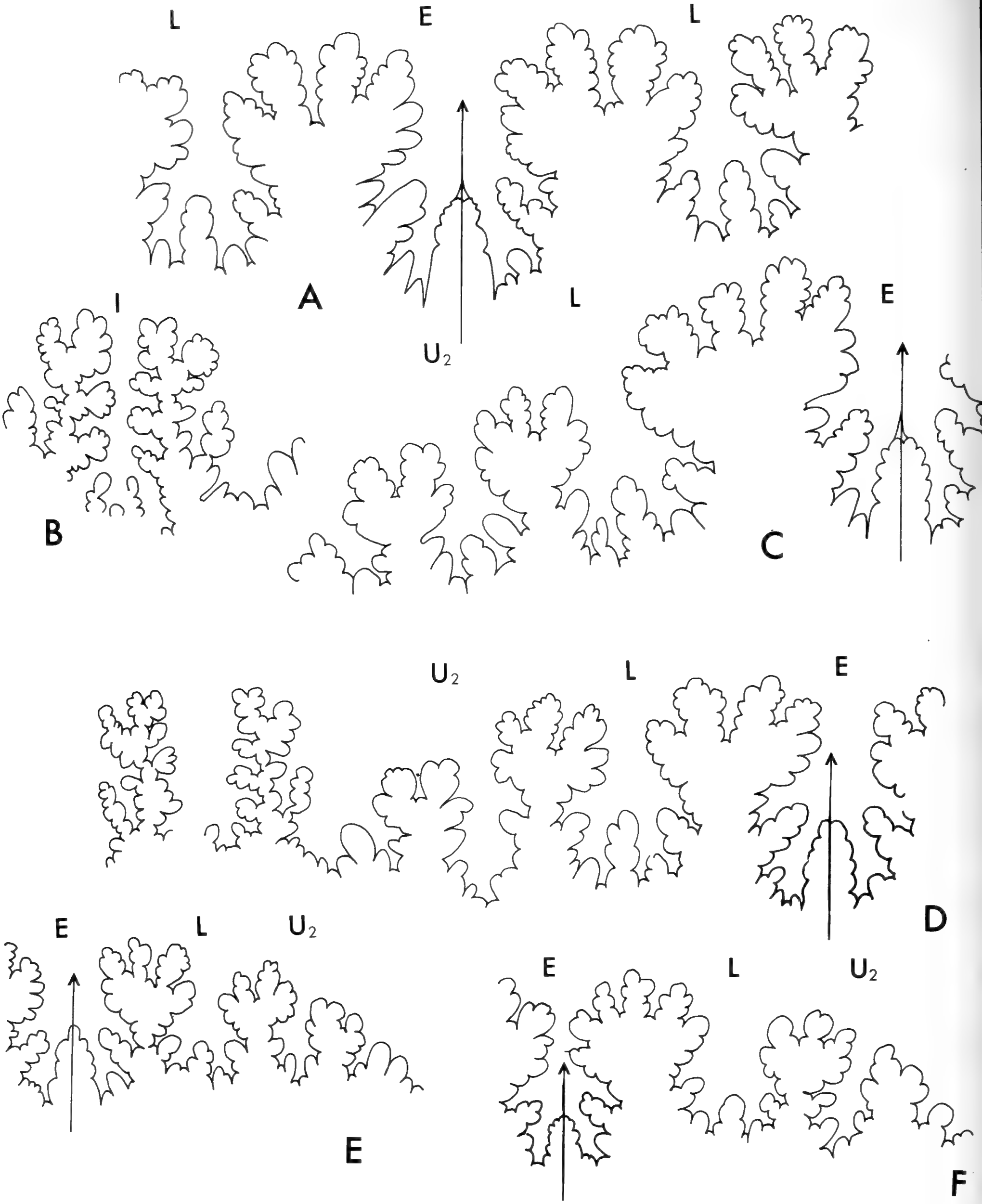

Fig. 15. External and internal sutures of *Saghalinites cala* (Forbes). A–E. BMNH C78545. F. BMNH 78844. All × 6.

the attachment of the siphuncle to the shell, but again there is no convincing evidence for this.

Occurrence

Saghalinites cala is common in Zululand, ranging from the Upper Campanian (Campanian IV) to the Lower Maastrichtian (Maastrichtian II). The doubtful Pondoland occurrence cannot be dated more precisely than Late Santonian to Early Campanian. The type, from southern India, is of Santonian or Campanian age, whilst there are also records from the Campanian of Antarctica and the ?Santonian of Tunisia.

Saghalinites nuperus (Van Hoepen, 1921)

Figs 16A–E, 17A–B, 18

Tetragonites cf. *cala* Yabe, 1915: 16, pl. 1 (fig. 7), pl. 3 (fig. 2).
Tetragonites nuperus Van Hoepen, 1921: 13, pl. 3 (figs 3–4), text-fig. 8. Besairie, 1930: 224, pl. 21 (fig. 3–3a).
Tetragonites cala Basse, 1931: 17, pl. 1 (figs 27–28), pl. 10 (fig. 7).
Saghalinites nuperus Collignon, 1956: 95, pl. 11 (fig. 1a–b); 1966: 3, pl. 456 (fig. 1856); 21, pl. 463 (fig. 1893).

Type

The holotype is TM 532, the original of Van Hoepen (1921, pl. 3 (figs 3–4)) by original designation.

Material

In addition to the holotype, the authors have seen three paratypes, TM 536 and 539, both from the Umzamba Formation of Late Santonian to Early Campanian age, locality 1, the mouth of the Umzamba River, Transkei (Pondoland), and a specimen, BMNH C78839, from locality 84, False Bay, Zululand (Santonian I).

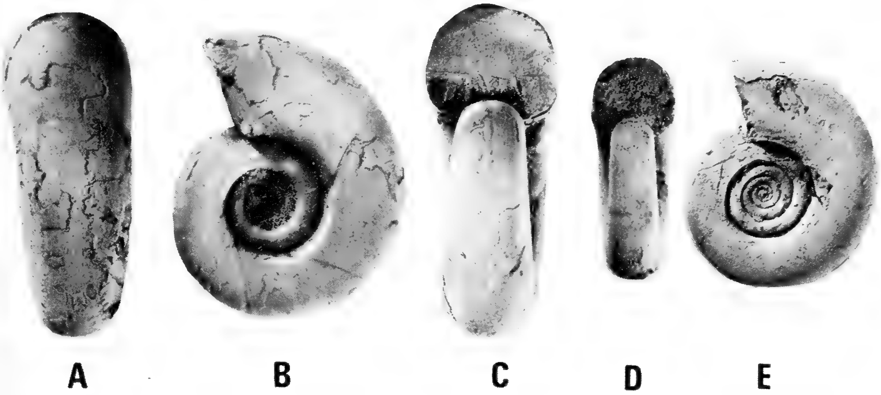

Fig. 16. *Saghalinites nuperus* (Van Hoepen). A–B. The holotype, TM 532. C–E. Paratype, TM 535. Both specimens are from the Umzamba Formation, of late Santonian to early Campanian age at locality 1, the mouth of the Umzamba River, Pondoland. × 1.

Dimensions

	D	*Wb*	*Wh*	*Wb/Wh*	*U*
Holotype	37,6	15,0(40)	14,0(37)	1,1	15,5(41)
Paratype TM 539	25,2	10,2(40)	9,0(35)	1,13	10,6(42)
Paratype TM 536 (crushed)	15,0	6,0(40)	5,6(37)	1,1	6,2(41)
BMNH C78839	92,0	42,0(46)	35,8(39)	1,17	32,5(35)
From Collignon 1955: 95					
MHNP 2173	53,0	21,0(40)	19,0(36)	1,1	21,0(40)
MHNP 2177	59,0	25,0(42)	21,0(36)	1,19	27,0(46)
MHNP 2179	72,0	31,0(43)	25,0(35)	1,24	30,0(42)

Description

Early whorls, 10–30 mm

The shell is of medium size, evolute, only 25 per cent of the previous whorl being covered, slowly expanding, with a wide umbilicus (*ca.* 40% of diameter). The whorl section is rounded at first in the smallest paratypes, but is depressed throughout later growth, becoming somewhat less depressed as diameter increases; the greatest breadth is a little below mid-flank. The umbilicus is shallow, with a low subvertical wall which merges into a rounded shoulder, which in turn grades imperceptibly into the rounded convergent flanks. The venter is broadly rounded.

The test is ornamented by very fine, dense striae which arise at the umbilical seam, run at first normal to the seam but then sweep strongly forwards over the shoulder and are gently convex and strongly prorsiradiate on the flanks. They sweep gently back across the ventro-lateral shoulder to form a gentle concave ventral sinus. The internal mould is smooth. Four to five constrictions per whorl are present, and occur from a diameter of 5 mm onwards, although initially rather faint. They are rather narrow, and follow a course parallel to the growth striae. On the test, their site is marked by a faint collar.

Adults

The larger specimen, 98,5 mm in diameter, is the largest described individual referred to this species and appears to be adult. The coiling is moderately involute, with depressed whorls and a moderately high expansion rate, a relatively deep umbilicus equal to 35 per cent of the diameter, with a high, subvertical wall. The umbilical shoulder is fairly abruptly rounded, the flanks gently inflated, convergent, with the greatest breadth some way below mid-flank. The ventrolateral shoulders are rounded, merging imperceptibly with a fairly broad, rounded venter. The test is ornamented by fine, dense striae, of rather variable strength. These arise at the umbilical seam, run normally across the inner part of the umbilical wall, but sweep strongly forwards on the shoulder. They are straight and strongly prorsiradiate on the inner flank, weakly convex at mid-flank, flexed gently backwards across the shoulder and pass across the venter with a slight convex peak. There are five well-developed constrictions on the last half-whorl, which run parallel to the growth striae. On the mould they are relatively deeply incised at the umbilical shoulder, and are narrow and sharply demarcated on flank and venter. They are rather less prominent on the test.

The suture line (Fig. 18) is rather simple, with a large, trifid first lateral saddle (E/L) and a smaller, virtually identical second lateral saddle (L/U_2). The lateral lobe (L) is bifid, the first auxiliary lobe trifid. The suspensive lobe is retracted with several auxiliaries.

Discussion

The holotype and paratypes of this species are rather small, but the larger individuals figured by Collignon (1956, 1966) and the present adult specimen

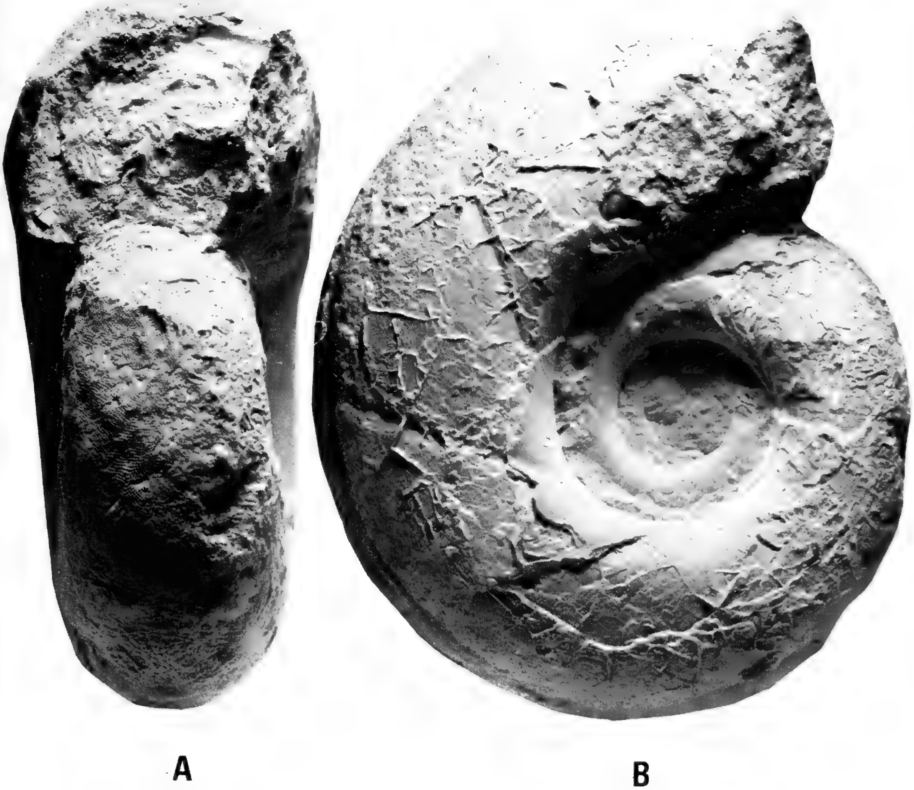

Fig. 17. *Saghalinites nuperus* (Van Hoepen). BMNH C78839, from the St Lucia Formation, Santonian I, locality 84, False Bay, St Lucia, Zululand. × 1.

show that this species retains a rounded whorl section throughout ontogeny, whilst constrictions become more closely spaced as diameter increases.

Saghalinites nuperus is thus readily separated from *S. cala* and *S. wrighti*, both these species developing a polygonal whorl section at large diameters. The constrictions of *S. cala* are, in addition, markedly flexed with a concave ventral sinus, rather than the peaked constrictions of the adult *S. nuperus*.

Saghalinites kingianus is a difficult species to interpret, being based upon a composite drawing taken from more than one specimen. It appears, however, to lack constrictions to a diameter of 40–50 mm, and when they do appear they are strongly prorsiradiate and straight rather than gently curved as in *S. nuperus*. Until further material is described and adequately figured, *S. kingianus* is perhaps best regarded as a *nomen dubium*.

Paulcke's *Saghalinites kingianum* var. *involutor* (1906: 175, pl. 17 (figs 3–4)) is based on two juveniles having the following dimensions:

	D	*Wb*	*Wh*	*Wb/Wh*	*U*
Example 1	11,0	9,0(81)	6,0(54)	1,5	3,5(31)
Example 2	22,0	17,0(77)	12,0(55)	1,42	7,0(32)

It thus differs markedly from *S. nuperus* in relative proportions and, like the typical form, lacks constrictions at this size.

Occurrence

The type material from Pondoland is from an unknown horizon within the Umzamba Formation of Late Santonian to Early Campanian age. Detailed collecting by one of the authors (H.C.K.) at the type section yielded one fragment of *S. nuperus* in the uppermost Santonian just below the Santonian/Campanian boundary. The species is also recorded from the Lower and Middle Santonian and possibly the Upper Santonian/Lower Campanian of Madagascar, and is known from the 'Senonian' of Japan.

Genus *Pseudophyllites* Kossmat, 1895

Type species

Ammonites indra Forbes, 1846 by original designation.

Diagnosis

Tetragonitids with moderately involute whorls when young, expanding to become very involute when adult. Early whorls depressed, with greatest breadth close to mid-flank, later whorls becoming rounded and varying from slightly compressed to slightly depressed. No constrictions; surface of test ornamented by fine transverse growth lines and spiral striae which combine to produce a typical reticulate pattern. Suture very finely divided with asymmetrically trifid or asymmetrically bifid major saddles having subphylloid terminations; suspensive lobe retracted.

Discussion

Pseudophyllites is readily separated from *Saghalinites* Wright & Matsumoto, 1954 in that that genus is very evolute, has a low expansion rate, a rounded to polygonal whorl section, a simpler suture line and prominent constrictions. *Tetragonites* Kossmat, 1895 typically has a rounded to squarish whorl section, a simpler suture, and generally bears striking constrictions throughout ontogeny.

The origin of *Pseudophyllites* clearly lies in *Tetragonites*, from which it evolved in the Late Santonian. Collignon (1956) lists six species which have been referred to that genus, and a further species, *Pseudophyllites skoui* Birkelund (1965: 37, pl. 3 (figs 2–6), text-figs 26–33), has since been added. Species are separated chiefly upon details of whorl section and suture line.

Occurrence

Pseudophyllites species are best known from the Campanian and Maastrichtian, the geographic distribution including Antarctica, South Africa, Madagascar, southern India, New Zealand, northern Australia, Japan, Sakhalin, southern and central Europe, west Greenland, Alaska, British Columbia, California and Brazil. The genus is also said to occur in the upper Santonian of Madagascar (Collignon 1956).

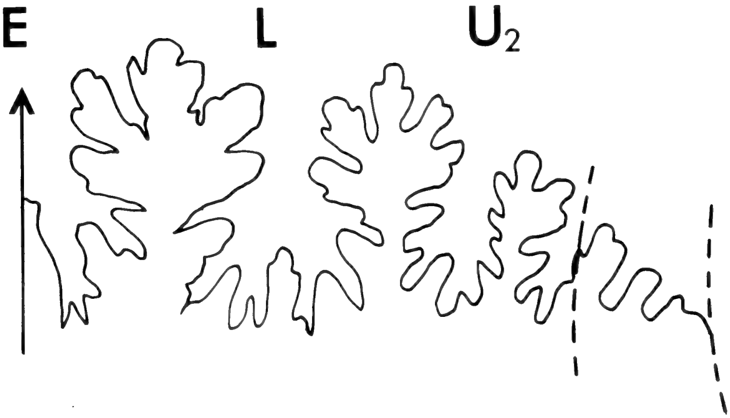

Fig. 18. *Saghalinites nuperus* (Van Hoepen). External suture of TM 532. × 10.

Pseudophyllites indra (Forbes, 1846)

Figs 19A–F, 20–22

Ammonites indra Forbes, 1846: 105, pl. 11 (fig. 7). Stoliczka, 1865: 112, pl. 58 (fig. 2a–b). Whiteaves, 1879: 105, pl. 13 (fig. 2–2a).

?*Gaudryceras colloti* De Grossouvre, 1894: 229, pl. 27 (fig. 8a–b).

Pseudophyllites indra Kossmat, 1895: 137, pl. 16 (figs 6–9), pl. 17 (figs 6–7), pl. 18 (fig. 3). Whiteaves, 1903: 331. Woods, 1906: 334, pl. 41 (fig. 6a–b). ?*Non* Kilian & Reboul, 1909: 14, text-fig. 3 = ?*P. latus*. Spath, 1921*b*: table opposite page 50; 1922: 119 (*pars*). *Non* Marshall, 1926: 152, pl. 20 (fig. 1), pl. 29 (figs 3–5) = *P. latus*. Nagao & Saito, 1934: 359, text-fig. 10. Collignon, 1938: 24, text-fig. E. Usher, 1952: 57, pl. 3 (figs 2–13), pl. 21 (fig. 17). Collignon, 1956: 90. Matsumoto, 1959: 134. Jones, 1963: 25, pl. 7 (figs 6–7), pl. 8, pl. 29 (figs 7–12), text-fig. 10. Collignon, 1969: 12, pl. 516 (fig. 2032).

Lytoceras indra Boule, Lemoine & Thévenin, 1906: 2, pl. 1 (fig. 1–1b).

Tetragonites virgulatus Van Hoepen, 1921: 11, pl. 3 (figs 1–2), text-fig. 7.

?*Pseudophyllites amphitrite* Maury, 1930: 167, pl. 27 (fig. 1), pl. 28 (fig. 1).

Parapachydiscus catarinae Anderson & Hanna, 1935: 19 (*pars*), pl. 3 (figs 2–3).

Pseudophyllites aff. *indra* Spath, 1940: 43.

Type

Lectotype herein designated, BMNH C51068, figured by Forbes (1846, pl. 11 (fig. 7)) from the Valudayur Group near Pondicherry, southern India.

Material

Six specimens, BMNH C19417 and C19418, TM 531 and 526 (the latter two being the types of *Tetragonites virgulatus* Van Hoepen) from the Late Santonian to Early Campanian, Umzamba Formation at locality 1, the mouth of the Umzamba River, Transkei (Pondoland), SAS H126/2 from locality 106 at the mouth of the Nyalazi River (Campanian I), and SAS H150, from locality 16, south of Mtubatuba (age uncertain).

Dimensions

		D	*Wb*	*Wh*	*Wb*/*Wh*	*U*
Lectotype						
BMNH C51068	at	109,3	—	61,5(56)	—	19,4(17)
	at	94,5	44,5(47)	50,0(53)	0,89	15,5(16)
C19417		296,0	148,5(50)	171(57)	0,87	42,0(14)
C19418		70,5	—	35,7(51)	—	13,0(18)
H126/2	at	98,5	53,0(54)	51,5(52)	1,02	18,6(18)
	at	77,5	40,3(52)	43,8(56)	0,92	14,3(18)
H150		109,0	60,0(55)	60,0(55)	1,0	—

Description

The coiling is very involute, rapidly expanding, typically with a compressed whorl section. The umbilicus is small and deep, conical, with a flat, outwards sloping wall. The umbilical shoulder is abruptly rounded, with initially rather flattened, convergent flanks, and an arched, rounded venter. The test is ornamented by fine striae and ridges which arise at the umbilical seam, sweep slightly backwards across the umbilical wall, flex backwards over the shoulder, pass across the flanks in a prorsiradiate direction and may be faintly convex. They sweep backwards across the ventro-lateral shoulder, and cross the venter with a broad, faint, concave ventral sinus. In addition, there are faint, closely spaced spiral striae which combine with the transverse ornament to produce a reticulate pattern on the shell surface.

Internal moulds are smooth, or may bear faint traces of the reticulate ornament. The suture line (Fig. 22) is highly subdivided, with a rather variably sub-

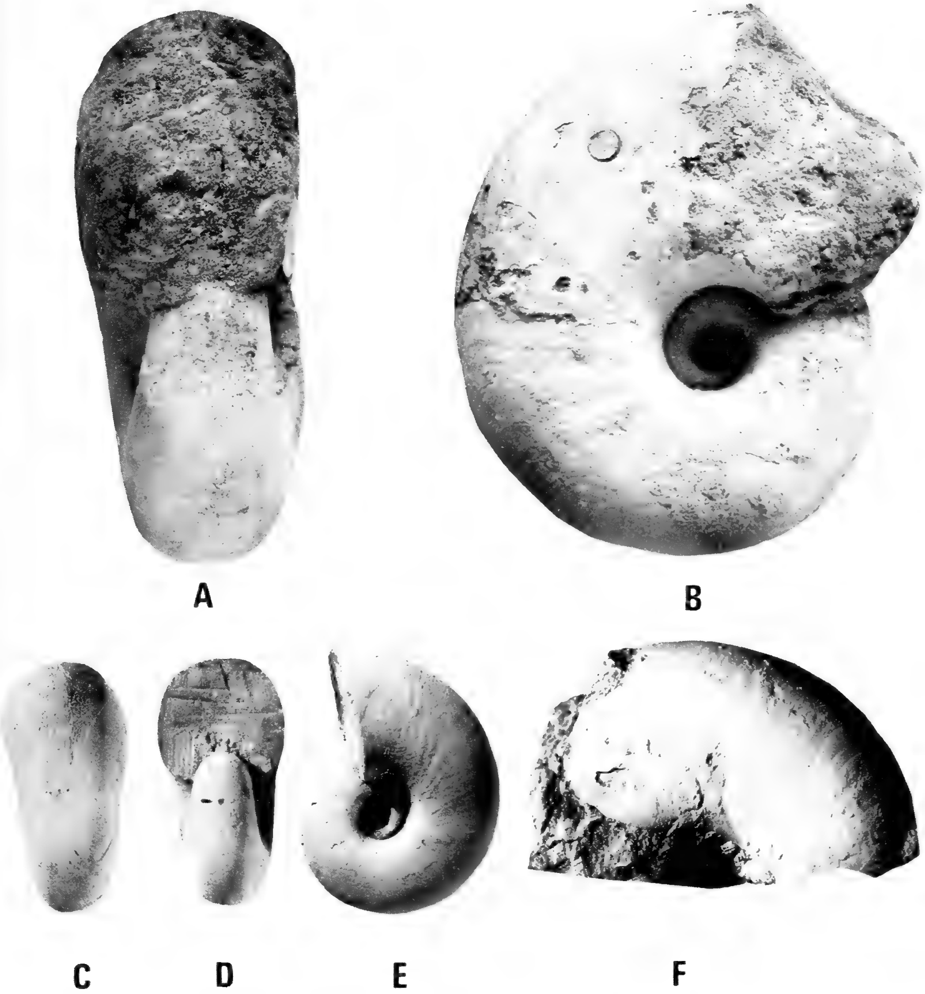

Fig. 19. *Pseudophyllites indra* (Forbes). A–B. BMNH C19418. C–E. TM 431, the holotype of *Tetragonites virgulatus* Van Hoepen. F. TM 526, a paratype of *T. virgulatus*. All specimens are from the late Santonian to early Campanian Umzamba Formation at locality 1, the mouth of the Umzamba River, Pondoland. × 1.

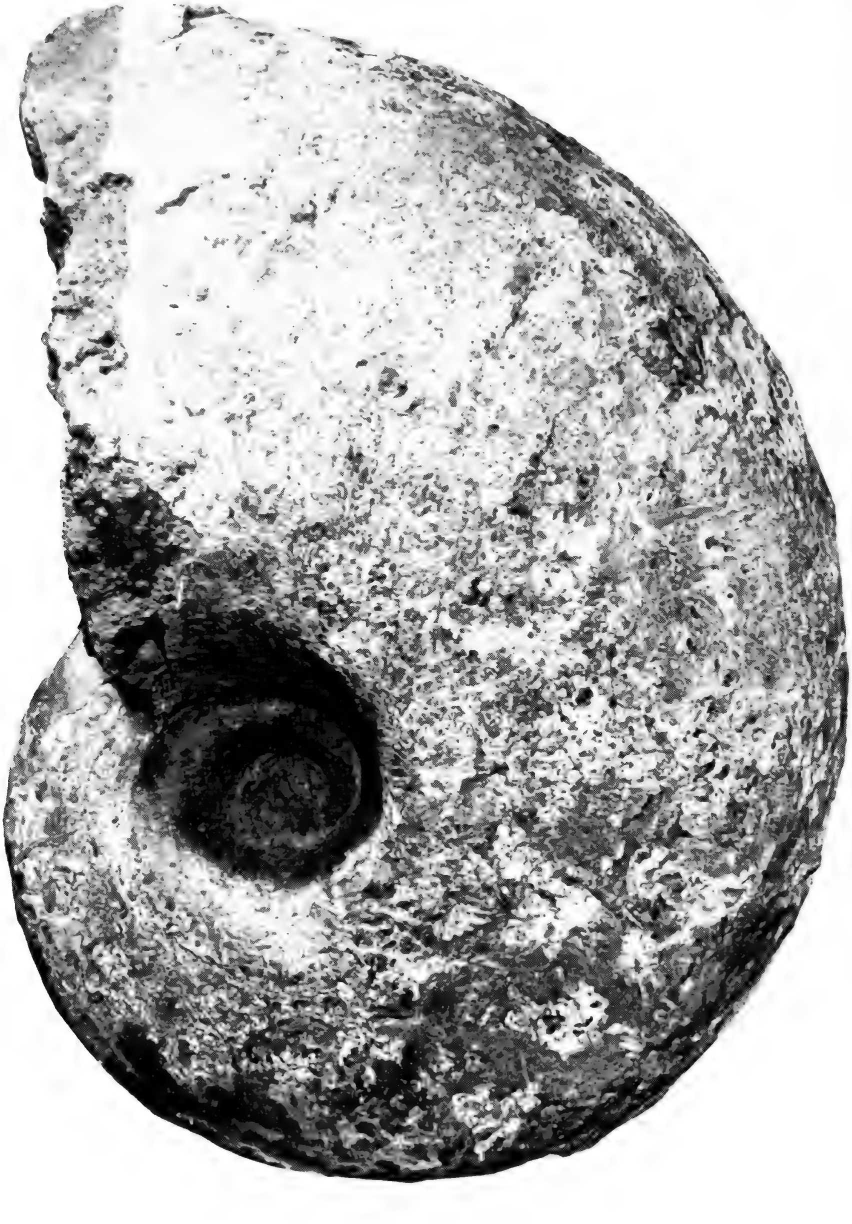

Fig. 20. *Pseudophyllites indra* (Forbes). BMNH C19417, from the Umzamba Formation, of late Santonian to early Campanian age at locality 1, the mouth of the Umzamba River, Pondoland. Reduced × 0,5. (British Museum photograph.)

Fig. 21. *Pseudophyllites indra* (Forbes). BMNH C19417, from the Umzamba Formation, of late Santonian to early Campanian age at locality 1, the mouth of the Umzamba River, Pondoland. Reduced × 0,5. (British Museum photograph.)

divided ventral saddle (E) which is often lanceolate in broad outline, a large, irregularly trifid first lateral saddle (E/L), a smaller bifid, second lateral saddle (L/U_2), a deeply incised bifid lateral lobe (L) deeper than the ventral lobe (E), and a retracted suspensive lobe with a large bifid first auxiliary saddle. Saddle terminations are typically subphylloid. The septal face shows two lateral saddles on either side of the internal lobe, and there is a massive septal lobe, well displayed on several of the present specimens.

Discussion

This classic species is characterized by a high expansion rate and rapid increase in whorl height, flattened flanks, fairly narrow venter, and a small, conical umbilicus in which the umbilical wall slopes outward to an abruptly rounded umbilical shoulder.

Pseudophyllites latus (Marshall) (1926: 152, pl. 20 (fig. 1), pl. 29 (figs 3–5)), of which *Pseudophyllites whangaroaensis* (Marshall) (1926: 153, pl. 20 (fig. 2), pl. 21 (fig. 11), pl. 32 (figs 5–6)), *Pseudophyllites peregrinus* Spath (1953: 7, pl. 1 (figs 6–9)) and *Pseudophyllites skoui* Birkelund (1965: 37, pl. 3 (figs 2–6), text-figs 26–33) are synonyms, is a species known from the Campanian to Maastrichtian of New Zealand, Antarctica, Madagascar and Greenland. From Henderson's (1970: 12 et seq.) recent discussion this form has a generally broader venter than *P. indra*, but shows identical ontogenetic changes and style of shell ornament. The sutures are said to differ, however, the ventral saddle of *P. indra* being lanceolate, that of *P. latus* being spatulate. The umbilical walls also differ, that of *P. indra* sloping distinctly outwards, that of *P. latus* being subvertical.

P. teres (Van Hoepen), a species based chiefly on small specimens, has been separated from *P. indra* on the basis of the compressed, flattened and subparallel flanks and consequently subrectangular whorl section, whilst the umbilical wall is subvertical.

Gaudryceras colloti De Grossouvre (1894: 229, pl. 37 (fig. 8a–b)) from the Upper Campanian of the Basses-Pyrenées, in southern France, is based upon a specimen just under 60 mm in diameter, with the following proportions:

D	*Wb*	*Wh*	*Wb/Wh*	*U*
58,0	27,0(46)	29,5(51)	0,92	10,5(18)

It is preserved as a composite mould, and is deformed. The ornament is of *Pseudophyllites* type, and it is best regarded as a synonym of *Pseudophyllites indra*.

Ammonites postremus Redtenbacher (1873: 115, pl. 26 (fig. 3a–d)) is based upon a series of specimens, the figure showing what may be a *Pseudophyllites*. It has a subrectangular whorl section and vertical umbilical wall; both features clearly separate it from *P. indra*.

Tetragonites virgulatus Van Hoepen (1921: 11, pl. 3 (figs 1–2), text-fig. 7) is based on juvenile *P. indra*; the types are figured here as Figure 19C–E.

Pseudophyllites amphitrite Maury (1930: 167, pl. 27 (fig. 1), pl. 28 (fig. 1)) is based upon a specimen having the following dimensions:

D	*Wb*	*Wh*	*Wb/Wh*	*U*
210	75(35)	120(51)	0,63	45(21)

The ornament matches that of *P. indra*, whilst there is a comparable ventral profile. The whorls are highly compressed, however, but this appears to be due to *post-mortem* crushing; the species is also best considered a synonym of *P. indra*. *Pseudophyllites nereidideditus* Maury (1930: 169, pl. 29 (fig. 1)) appears to be a crushed *Pseudophyllites teres*, as discussed below. The umbilicus and relative proportions readily separates it from *P. indra*.

Occurrence

Pseudophyllites indra ranges from the late Santonian to early Maastrichtian. Its geographic distribution includes South Africa (Zululand and Pondoland), Madagascar, southern India, northern Australia, Japan, Sakhalin, Alaska, British Columbia, California and possibly south-eastern France and Brazil.

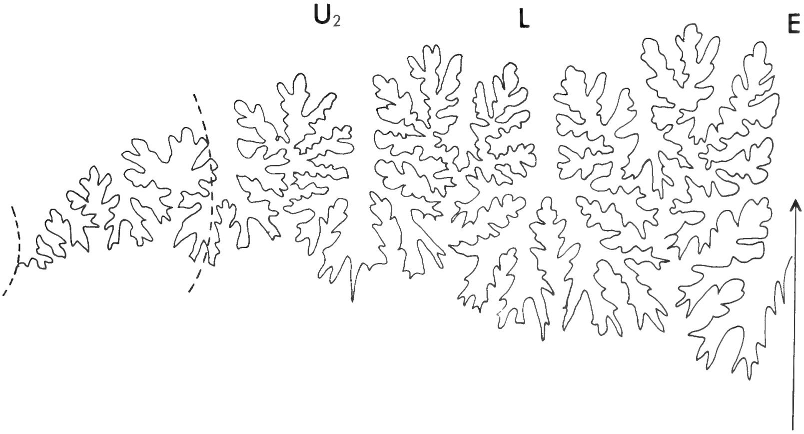

Fig. 22. External suture of *Pseudophyllites indra* (Forbes). TM 531. × 5.

Pseudophyllites teres (Van Hoepen, 1920)

Figs 23A–B, 24A–B

Tetragonites teres Van Hoepen, 1920: 144, pl. 25 (figs 1–2).
Pseudophyllites indra Spath, 1922: 119 (*pars*).
?*Pseudophyllites nereidideditus* Maury, 1930: 169, pl. 29 (fig. 1).
Pseudophyllites teres Collignon, 1956: 94, pl. 9 (fig. 2–2b); 1969: 14, pl. 517 (fig. 2034).

Type

The holotype is Van Hoepen's original specimen, TM 562, by original designation.

Material

Two specimens, the holotype and BMNH C19415, both from the late Santonian to early Campanian Umzamba Formation at locality 1, the mouth of the Umzamba River, Pondoland.

Dimensions

		D	*Wb*	*Wh*	*Wb/Wh*	*U*
Holotype						
TM 562	(*a*)	69	—	39(57)	—	14(20)
	(*b*)	57	26(46)	31(54)	0,84	—
From Collignon (1956: 94)						
MHNP 2160		51,0	25,0(49)	26,0(51)	0,96	11,0(22)
MHNP 2163		78,0	39,0(50)	42,0(54)	0,93	16,0(21)
MHNP 2164		98,0	43,0(44)	52,0(53)	0,83	19,0(19)
MHNP 2166		115,0	54,0(47)	63,0(55)	0,86	21,0(18)

Description

The coiling is involute, rapidly expanding, and compressed (whorl breadth to whorl height ratio is less than 0,96, decreasing with age). The umbilicus is small (20 % of diameter), deep, with a high, subvertical wall and abruptly rounded

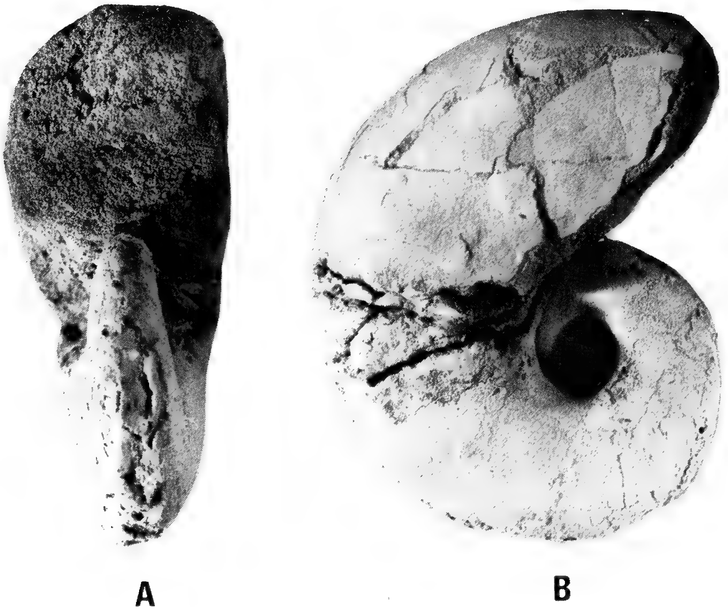

Fig. 23. *Pseudophyllites teres* (Van Hoepen). TM 535, the holotype from the Umzamba Formation, of late Santonian to early Campanian age, locality 1, the mouth of the Umzamba River, Pondoland. × 1.

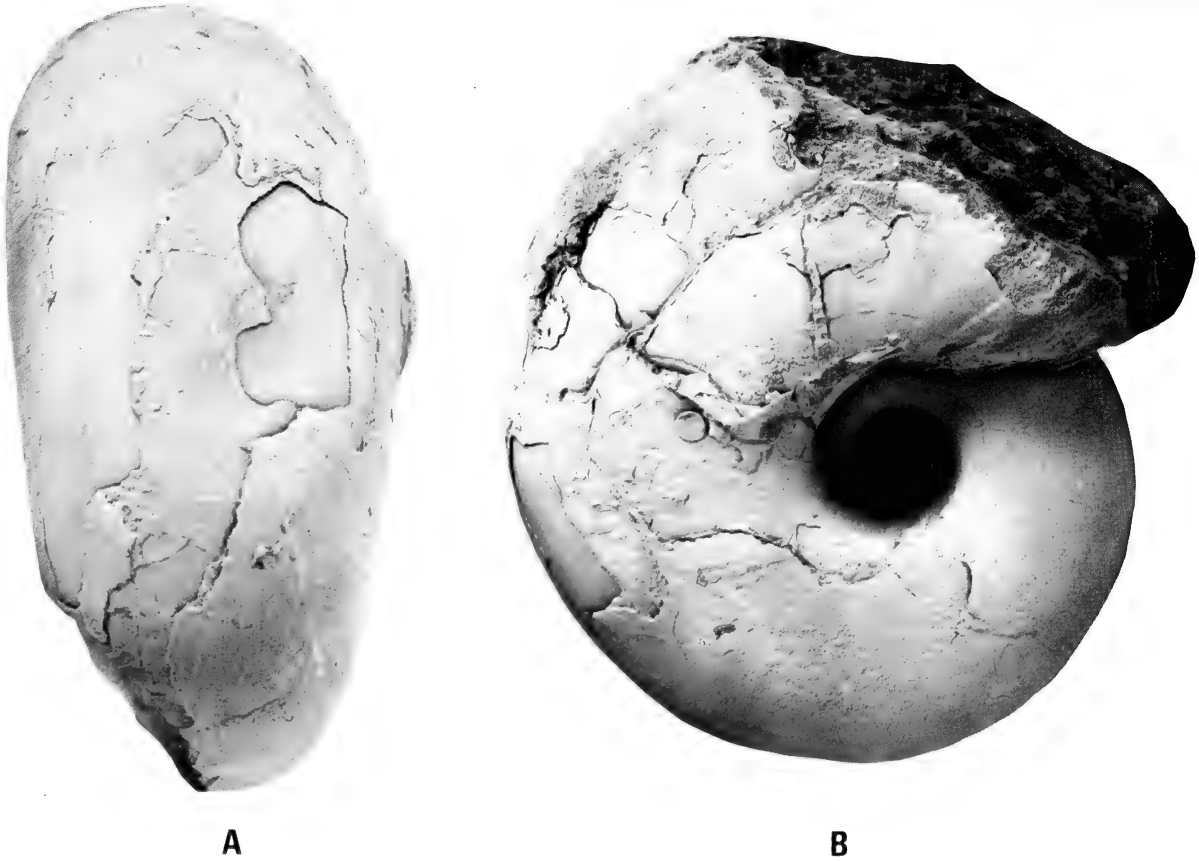

Fig. 24. *Pseudophyllites teres* (Van Hoepen). BMNH C14915, from the Umzamba Formation, of late Santonian to early Campanian age, locality 1, the mouth of the Umzamba River, Pondoland. × 1.

shoulder. The greatest breadth is at the umbilical margin, the inner flanks being flattened and subparallel, with broadly rounded shoulders and venter. Ornament is not well preserved, but consists of fine, dense growth striae which pass back across the umbilical wall, sweep forwards over the shoulder and are strongly prorsiradiate and faintly convex on the flank, passing backwards across the shoulder and running almost normally across the venter.

There is a marked apertural constriction. The suture line is poorly visible, but of the *Pseudophyllites* type.

Discussion

The largest specimens the authors have seen of this species are adult at approximately 100 mm diameter, and at this size the compressed whorls with flattened, subparallel sides, plus the umbilicus with subvertical wall, clearly differentiates this species from *Pseudophyllites indra*, *P. latus* and *P. postrematus*. *Pseudophyllites nereidideditus* Maury (1930: 196, pl. 29 (fig. 1)) appears to be a large crushed example possibly referable to this species. The dimensions given by Maury are as follows:

D	*Wb*	*Wh*	*Wb/Wh*	*U*
210,0	70,0(33)	115,0(55)	0,61	45,0(21)

Occurrence

Santonian–Campanian of Pondoland (Umzamba Formation) and Madagascar. ? Maastrichtian of Brazil.

Pseudophyllites latus (Marshall, 1926)

Figs 25–26

Pseudophyllites indra Kilian & Reboul, 1909: 14. Marshall, 1926: 152, pl. 20 (fig. 1), pl. 29 (figs 3–5).
Tetragonites latus Marshall, 1926: 149, pl. 20 (fig. 6), pl. 32 (figs 1–2).
Pseudophyllites whangaroaensis Marshall, 1926: 153, pl. 20 (fig. 2), pl. 21 (fig. 11), pl. 32 (figs 5–6).
Pseudophyllites peregrinus Spath, 1953: 7, pl. 1 (figs 6–9). Collignon, 1956: 92, text-fig. 12.
Pseudophyllites latus Henderson, 1970: 12, pl. 1 (fig. 10), pl. 2 (fig. 3), text-fig. 4a–c.
Pseudophyllites skoui Birkelund, 1965: 37, pl. 3 (figs 2–6), text-figs 26–33.

Type

The lectotype, designated by Henderson (1970: 14) is the original of Marshall (1926, pl. 32 (fig. 1)), from the Mata Series (Campanian) of New Zealand.

Material

One specimen only, SAS Z1114, from locality 106 at the mouth of the Nyalazi River (Campanian I).

Dimensions

	D	*Wb*	*Wh*	*Wb/Wh*	*U*
SAS Z1114	172,0	96,4(56)	94,8(55)	1,02	28,5(17)
From Collignon (1956: 93)					
MHNP 2152	80,0	44,0(55)	40,0(50)	1,1	16,0(20)
MHNP 2154	90,0	51,0(57)	48,0(53)	1,1	16,0(18)
MHNP 2155	127,0	73,0(57)	69,0(54)	1,05	24,0(19)
MHNP 2157	181,0	113,0(62)	101,0(56)	1,1	33,0(18)

Fig. 25. *Pseudophyllites latus* (Marshall). SAS Z1114, from the St Lucia Formation, Campanian I, locality 106, at the mouth of the Nyalazi River, Zululand. × 0,8.

Description

The specimen is wholly septate, and retains much of the original aragonitic shell. The coiling is very involute, more than four-fifths of the previous whorl being covered, with a slightly depressed whorl section throughout ontogeny. The whorls expand rapidly, the greatest breadth being at the umbilical shoulder. The umbilicus is deep, conical and narrow (17% of diameter), with a high, flat,

Fig. 26. *Pseudophyllites latus* (Marshall). SAS Z1114, from the St Lucia Formation, Campanian I, locality 106, at the mouth of the Nyalazi River, Zululand. The specimen shows the reticulate ornament clearly, and has the septal lobe well preserved. × 0.8.

subvertical wall. The umbilical shoulder is abruptly rounded, the flanks broadly rounded and convergent, merging with a broadly rounded venter. Ornament consists of fine transverse growth striae and longitudinal ridges which combine to produce a reticulate pattern which is particularly conspicuous on the venter. The transverse striae arise at the umbilical seam, pass straight up the umbilical wall with a shallow concavity, are slightly prorsiradiate and weakly convex across the flanks, and sweep backwards across the ventrolateral shoulders to form a shallow, broad ventral sinus.

The suture consists of a broad, short, moderately subdivided spatulate ventral saddle, a massive, highly subdivided bifid first lateral saddle (E/L) and a smaller bifid second lateral saddle (L/U_2) separated by a symmetrical bifid lateral lobe (L) which is deeper than the external lobe (E). The suspensive lobe includes five or six auxiliary lobes; there are two internal saddles and a massive septal lobe (Fig. 26).

Discussion

P. latus is readily separated from *P. indra* on the basis of its broader whorls, less rapidly increasing height, and much steeper umbilical wall. It differs from *P. teres* in being broader and having convergent rather than subparallel flanks. The spatulate rather than lanceolate ventral saddle is also distinctive. *P. postrematus* has a distinctly rectangular whorl section, as noted above.

The authors agree with Henderson (1970) in regarding *Pseudophyllites peregrinus* Spath, *P. skoui* Birkelund and *P. whangaroaensis* Marshall as synonyms of *P. latus*.

Occurrence

Campanian of New Zealand and Antarctica, Upper Santonian and Campanian of Madagascar, Maastrichtian of Greenland, and Campanian of Zululand.

STRATIGRAPHY

The stratigraphic distribution in south-eastern Africa of the species described herein is illustrated in Figure 27.

ACKNOWLEDGEMENTS

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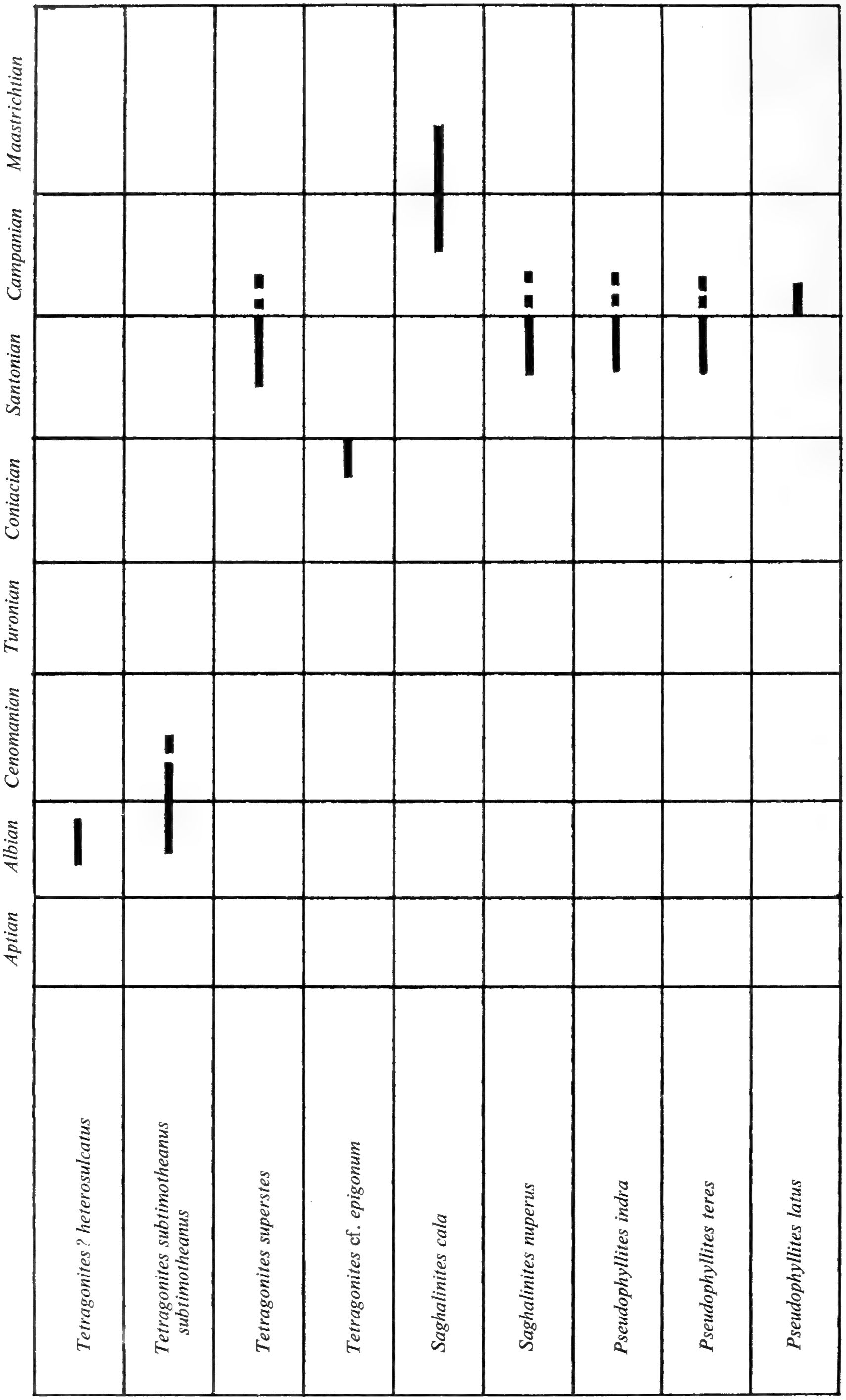

Fig. 27. Stratigraphic distribution of tetragonitids in south-east Africa.

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Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

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Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family **Nuculanidae**

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (figs 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:
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CRETACEOUS FAUNAS FROM ZULULAND AND NATAL, SOUTH AFRICA
THE AMMONITE FAMILY TETRAGONITIDAE HYATT, 1900

VOLUME 73 PART 8 AUGUST 1977 ISSN 0303-2515

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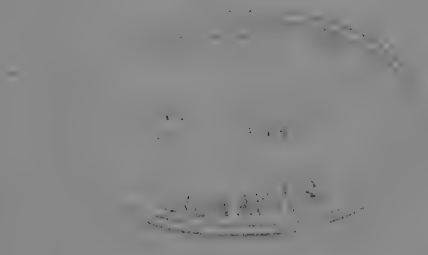

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NOTES ON THE SCORPION FAUNA OF THE CAPE

PART 2

THE *PARABUTHUS CAPENSIS* (EHRENBERG) SPECIES-GROUP; REMARKS ON TAXONOMY AND BIONOMICS (ARACHNIDA, SCORPIONIDA, BUTHIDAE)

By

E. B. EASTWOOD

South African Museum, Cape Town

(With 7 figures and 1 table)

[*MS. accepted 31 March 1977*]

ABSTRACT

Parabuthus neglectus Purcell was synonymized with *P. capensis* (Ehrenberg) by Hewitt in 1918. A re-examination of the types of these two species and material in the South African Museum collection revealed significant morphological and geographical differences. *P. capensis* is redescribed and *P. neglectus* is reinstated and redescribed. Distribution, morphology and habitat of these two species are discussed, with notes on a black form of *P. capensis*.

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INTRODUCTION

Androctonus capensis was originally described by Ehrenberg (1828), not Hemprich and Ehrenberg as is recorded in most literature. The original description is to be found in an account of the travels of Hemprich and Ehrenberg, hence the mistake made by subsequent workers in referring the description to both these people.

Purcell (1902) redescribed *P. capensis* from specimens in the South African Museum collection. Pocock (1902) compared the type of *P. planicauda* (Pocock) with Purcell's *capensis* and found them to be identical. He suggested that Purcell (1899) had redescribed *P. capensis* as *P. neglectus* and *P. planicauda* (Pocock) as *P. capensis* (Purcell 1902). Hewitt (1918) synonymized *P. neglectus* with *P. capensis*.

Ann. S. Afr. Mus. **73** (8), 1977: 199–214, 7 figs, 1 table.

In this paper *P. capensis* is redescribed with notes on its distribution and habitat, and a black form which is morphologically identical is discussed. *P. neglectus* is reinstated and redescribed, since the original description was inadequate, with notes on its distribution, morphology and habitat.

REDESCRIPTION

Parabuthus capensis (Ehrenberg, 1828)

HOLOTYPE FEMALE (Fig. 1)

Measurements are given in Table 1.

Colour

In the alcohol-preserved specimen the tergites, carapace and telson are dark reddish-brown, the cauda, sternites and legs yellowish-brown.

TABLE 1

Measurements in millimetres of *Parabuthus capensis* (Ehrenberg) and *P. neglectus* Purcell.

	P. capensis Holotype ♀	*P. neglectus* Lectotype ♂	*P. neglectus* Paralectotype ♀ ♀
Total length	73,6	79,0	88,0–100,0
Carapace length	8,6	6,0	6,5–8,2
width (max.)	9,0	6,8	7,0–9,5
width (min.)	5,5	4,0	3,5–6,0
Pedipalps			
Femur length	6,2	4,5	5,0–6,0
Patella length	6,8	4,8	5,2–7,0
Chela length	11,0	9,8	9,2–13,0
width	3,0	2,0	2,0–3,0
Movable finger length	7,9	5,0	6,1–8,2
Mesosoma length	18,2	19,5	19,2–21,0
Metasoma length	46,8	32,0	38,0–52,0
Caudal segment I			
length	6,0	5,0	4,0–7,0
width	5,8	4,0	4,0–6,0
Caudal segment II			
length	7,2	5,5	4,8–7,5
width	6,0	4,2	4,2–6,2
Caudal segment III			
length	7,2	5,5	4,8–8,0
width	6,0	4,2	4,2–6,0
Caudal segment IV			
length	8,0	6,0	5,0–7,8
width	6,0	4,0	4,5–6,0
Caudal segment V			
length	9,0	6,5	6,0–8,8
width	6,0	3,6	4,0–5,0

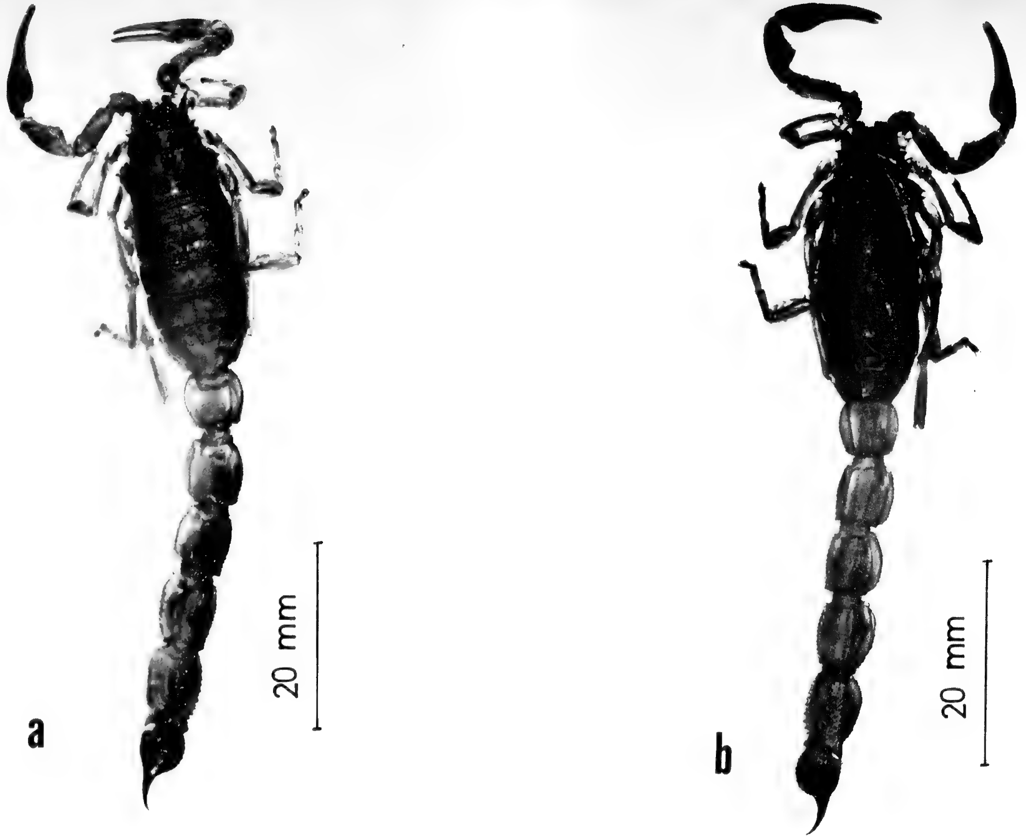

Fig. 1. a. Dorsal view of *Parabuthus capensis* (Ehrenberg), holotype female. b. Ventral view of *Parabuthus capensis* (Ehrenberg), holotype female.

Carapace

Slightly wider than long; anterior–posterior divergence 0,47; densely and finely granular throughout.

Tergites

Densely granular throughout, the granules becoming coarser posteriorly in each segment; median keel smooth, extending two-thirds the length of segments I to VI posteriorly; two pairs of strongly granular lateral keels on segment VII; a few short microtrichia on the lateral margins of segments I to VI.

Sternites

The last four segments smooth and polished; the last segment with sparse, rounded granules laterally; rows of microtrichia laterally and posteriorly on each segment.

Cauda

Segment I sparsely granular; ventral and ventrolateral keels smooth, lateral, dorsolateral and dorsal keels granular; dorsal stridulatory area extending the whole length and almost three-quarters of the breadth of the segment, with finely granular ridges laterally.

Segment II granular, ventral keels consist of long contiguous granules, terminal granule slightly enlarged, rounded; dorsal stridulatory area medially depressed; the posterodorsal edge of the segment is elevated and slightly curved forward medially, forming a subtriangular 'lip'.

Segment IV granular, dorsal keel granular, posteriorly continuous with the dorsolateral keel; accessory keel consists of 4–6 blunt granules; ventral keels posteriorly obsolete; dorsal surface medially depressed along its whole length, lightly shagreened medially with finely granular ridges laterally.

Segment V granular; the single ventral keel is posteriorly obsolete; well-developed ventrolaterals; dorsal keels well developed anteriorly; accessory keels represented by two or three low, rounded larger granules; dorsally the segment is smooth. Vesicle coarsely and sparsely granular.

The entire cauda is very sparsely setiferous.

Pedipalps

Femur finely granular, with a few larger granules internally; anterodorsal, anteroventral and posterodorsal keels distinctly granular. Patella finely granular; keels distinctly granular. Chela slender, movable finger with 12 inner flanking teeth; the median series consisting of 8–10 teeth, including the external lateral teeth of the outer series of each row; the distal end with 3 enlarged teeth.

Trichobothriotaxy

See Figure 4.

Pectines

30/30 teeth; the basal lamellae greatly enlarged and subrectangular in shape.

Operculum

Subcordiform; fused medially.

TYPE MATERIAL

Holotype female

ZMB 133. Cape of Good Hope, Lichtenstein legit., deposited at the Zoologisches Museum, Berlin, DDR.

Parabuthus neglectus Purcell, 1899

LECTOTYPE MALE (Fig. 2)

Measurements are given in Table 1.

Colour

In alcohol-preserved specimens the colour is yellow, the mesosoma and metasoma yellowish-brown.

Carapace

Wider than long; anterior–posterior divergence 0,5; densely and finely granular throughout.

Tergites

Densely and finely granular throughout, with coarser granulation on each segment posteriorly; median keel represented by a granular elevation in the middle of the first six segments; two pairs of strongly granular lateral keels on the seventh segment; fairly long microtrichia on the lateral and posterior margins of all segments.

Sternites

The last four segments smooth and polished; the last segment with sparse, rounded granules laterally; sparse rows of microtrichia laterally and posteriorly on all segments.

Cauda

Segment I sparsely granular; ventral and ventrolateral keels smooth; lateral, dorsolateral and dorsal keels well developed and granular; posterior granule of dorsal keel not enlarged; dorsal surface with a slightly concave shagreened area, extending the whole length and almost three-quarters of the breadth of the segment, laterally with finely granular ridges.

Segment II sparsely granular; ventral and ventrolateral keels consist of

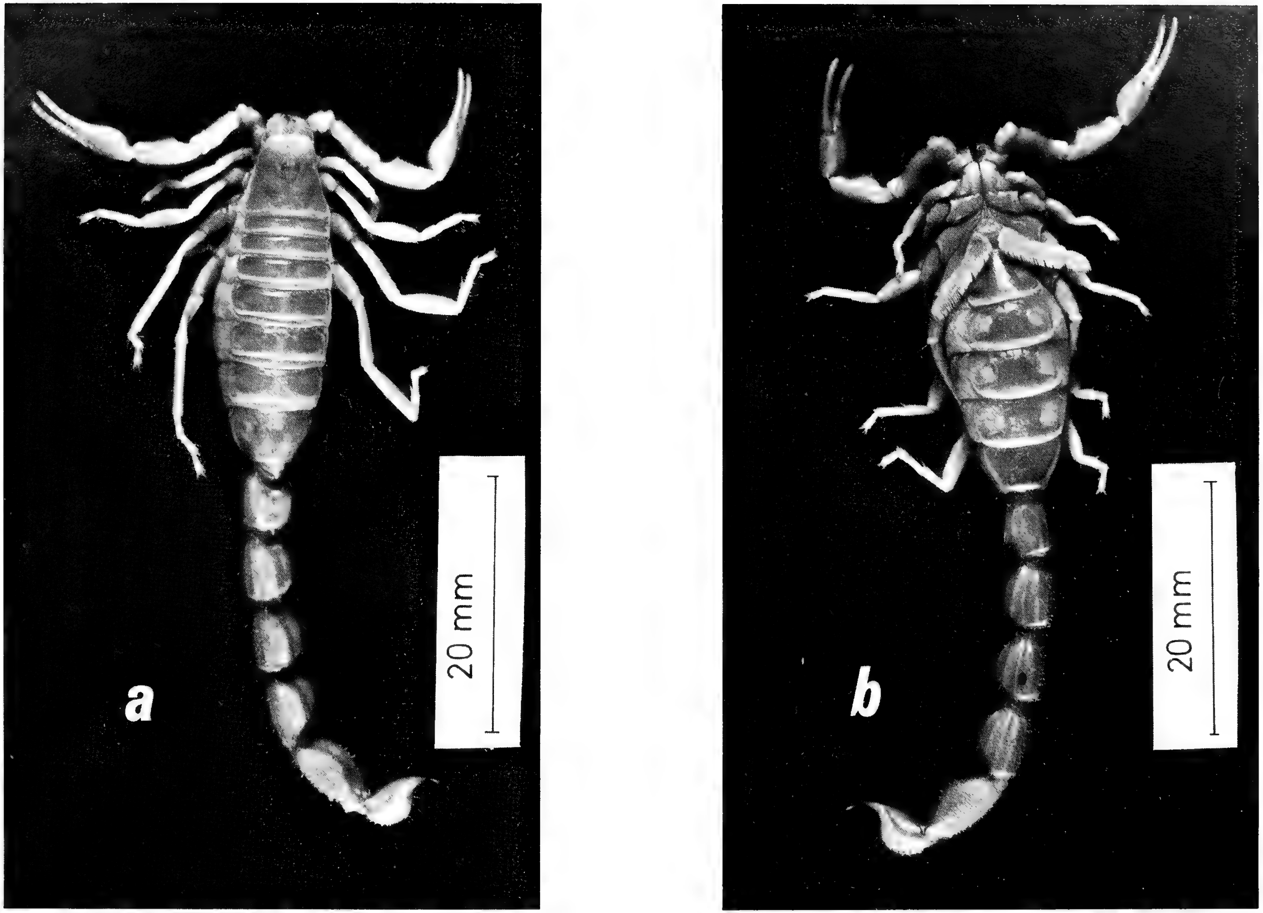

Fig. 2. a. Dorsal view of *Parabuthus neglectus* Purcell, lectotype male. b. Ventral view of *Parabuthus neglectus* Purcell, lectotype male.

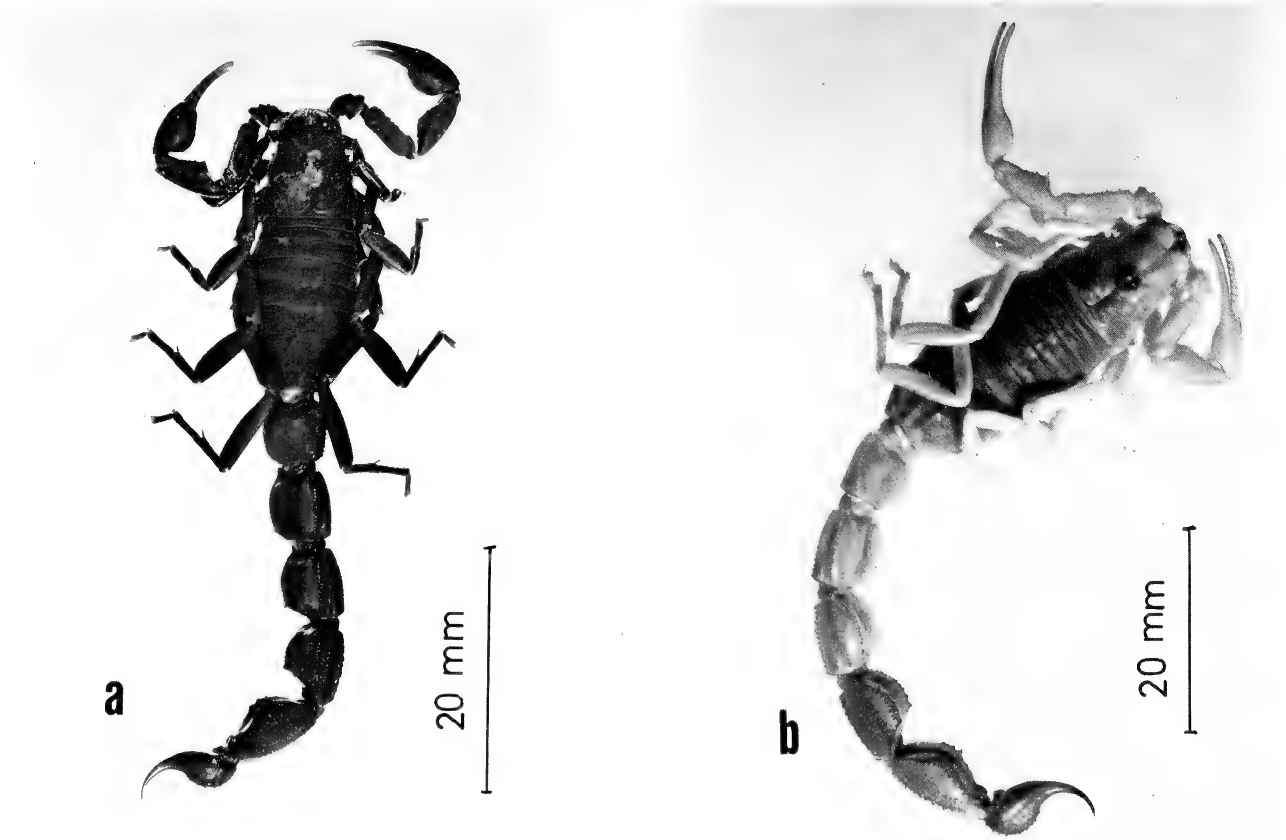

Fig. 3. a. Dorsal view of the black form of *Parabuthus capensis* (Ehrenberg), female. b. Dorsal view of *Parabuthus neglectus* Purcell, female from northern Namaqualand showing the darker coloration of the telson and last two caudal segments.

separate well-defined and prominent granules, increasing in size posteriorly; other keels not as well defined; dorsal surface with the shagreened area forming a deep depression; the posterodorsal edge of the segment is strongly elevated and curved forward medially, forming a very distinctly subtriangular 'lip'.

Segment III granular; keels well developed and granular; ventral and ventrolateral keels very prominent; the posterior granule of the dorsal keel slightly enlarged; the dorsal shagreened area forming a deep oval depression anteriorly; finely granular ridges laterally; the posterodorsal edge of the segment is curved forward medially to form a well-developed subtriangular 'lip'.

Segment IV granular; keels granular, not prominent; posterior granule of dorsal keel slightly enlarged; dorsal surface medially depressed along its whole length, lightly shagreened medially with finely granular ridges laterally.

Segment V granular; the single ventral keel distinct; well-developed ventrolaterals; dorsal keels well developed anteriorly, accessory keels represented by three or four sharply pointed spines; dorsally the segment is smooth.

Vesicle granular; ventrally some of the granules are very prominent. The metasoma is covered with long setae ventrally and laterally.

Pedipalps

Femur finely granular, with a few larger granules internally; anterodorsal, anteroventral and posterodorsal keels distinctly granular. Patella finely granular; keels distinctly granular. Chela slender, movable finger with 10 inner flanking teeth; the median series consisting of 6–10 teeth, including the external lateral teeth of the outer series of each row; the distal end with 3 enlarged teeth.

Trichobothriotaxy

See Figure 5.

Pectines

38/38 teeth; the basal lamellae not enlarged.

Operculum

Subcordiform; cleft longitudinally, with a pair of genital papillae below the operculum.

PARALECTOTYPE FEMALES

Measurements given in Table 1. Morphologically the same as the holotype except for the following:

Pectines

34–36 teeth, with basal lamellae greatly enlarged and subrectangular in shape.

Operculum

Subcordiform; fused medially.

TYPE MATERIAL

A lectotype was chosen from the syntypes designated by Purcell (1899).

Lectotype male

SAM–1197/1. Between Pakhuisberg and Oorlogskloof, Clanwilliam district, Cape. (32°0′S 19°15′E) M. Schlechter legit. 1897.

Paralectotypes

SAM–1197/2. 3 ♂♂, 11 ♀♀. Data as for lectotype. All type material deposited at the South African Museum.

DISCUSSION

The *P. capensis* group is distinguished from other species by having the postero-dorsal edge of caudal segments II and III curved forward medially, forming a subtriangular 'lip'.

P. capensis and *P. neglectus* are separable by the following combination of characters: the structure of the accessory keels of caudal segment V, the structure of the ventral and ventrolateral keels, and posterior dorsal lip of caudal segments II and III, the density and length of meso- and metasomal setae, and number of pectinal teeth. The distribution of trichobothria on the pedipalpal segments is orthobothriotaxic for both species (Figs 4–5), with little variation in position. These two species may be separated by the differences in characters set out in the key provided below.

KEY TO THE *PARABUTHUS CAPENSIS* SPECIES-GROUP

1. Granules of accessory keels of caudal segment V low and rounded; ventral and ventrolateral keels of caudal segments II and III consist of low, almost contiguous granules; posterior dorsal lip of caudal segments II and III not well developed; meso- and metasomal setae sparse and short; pectinal teeth 33–37 for males, 31–35 for females . . . . *capensis* (Ehrenberg)

— Granules of accessory keels of caudal segment V elongated and sharply pointed; ventral and ventrolateral keels of caudal segments II and III separate and prominent; posterior dorsal lip of caudal segments II and III well developed, extending well forward; meso- and metasomal setae long and fairly dense; pectinal teeth 36–38 for males, 35–36 for females . . . . *neglectus* Purcell

P. capensis is found in the south-western corner of the Cape in the winter-rainfall region, extending from Clanwilliam in the north to Cape Town in the south and eastwards to Tulbagh. In the north (Clanwilliam and Laaiplek), a form is found which is entirely black (see Fig. 3a). This form cannot be morphologically distinguished from the yellow form of *P. capensis* and ecological data give no indication that it is a distinct species. Specimens of the yellow form have been found under rocks or other debris in areas of hard-packed soil. The black forms from Laaiplek were found under rubbish on coastal sand dunes, while the specimen from Clanwilliam was found under a stone in a shallow burrow in an

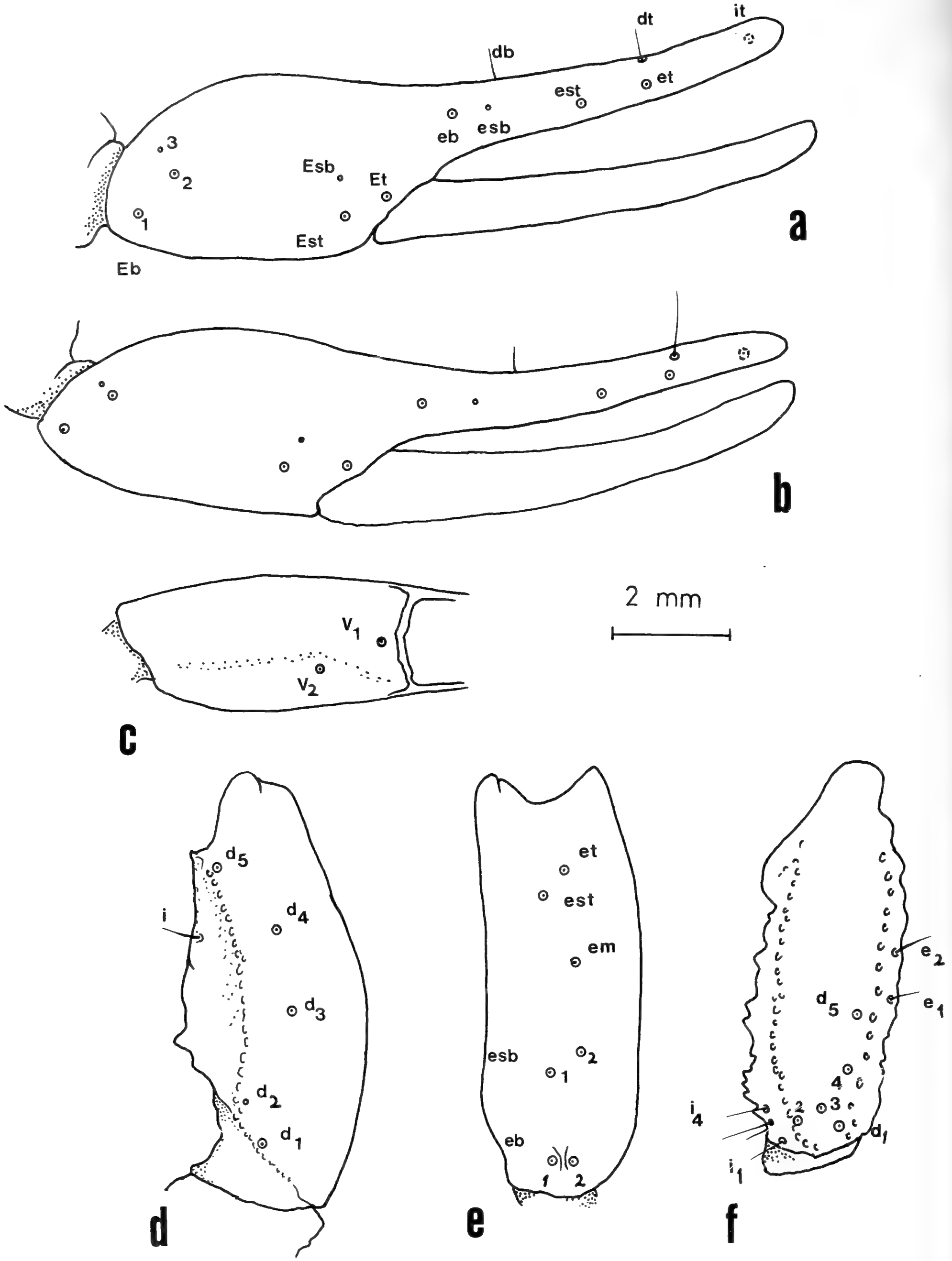

Fig. 4. Trichobothriotaxy of *Parabuthus capensis* (Ehrenberg). a. External aspect of male chela. b. External aspect of female chela. c. Ventral aspect of female chela. d. Dorsal aspect of patella. e. External aspect of patella. f. Dorsal aspect of femur.

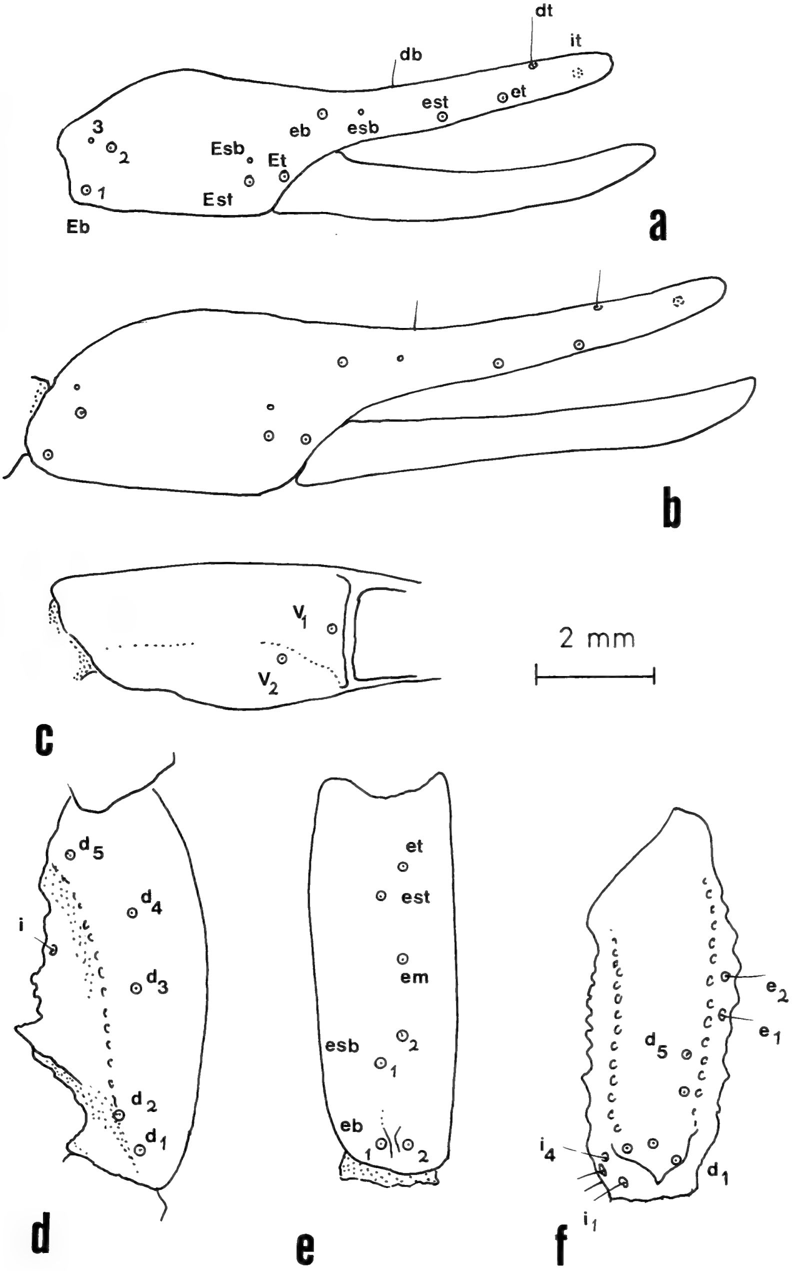

Fig. 5. Trichobothriotaxy of *Parabuthus neglectus* Purcell. a. External aspect of male chela. b. External aspect of female chela. c. Ventral aspect of female chela. d. Dorsal aspect of patella. e. External aspect of patella. f. Dorsal aspect of femur.

area of hard-packed soil. The author has found *P. capensis* in association with *Opisthophthalmus pallidipes* Koch, *O. capensis* (Herbst) and *Uroplectes carinatus* (Pocock).

A laboratory specimen of *P. capensis* has been observed to excavate a run beneath ground cover as follows: the tail was curved either sideways or directly over the mesosoma so that the telson lay above the carapace, and the first two pairs of walking legs were used in alternative scraping motions to loosen the sand. The body was then raised by stilting on the hind legs while the first two pairs of legs and sometimes the third pair scraped the sand very vigorously so that it sprayed out behind the scorpion; the pedipalps and fourth pair of legs were used

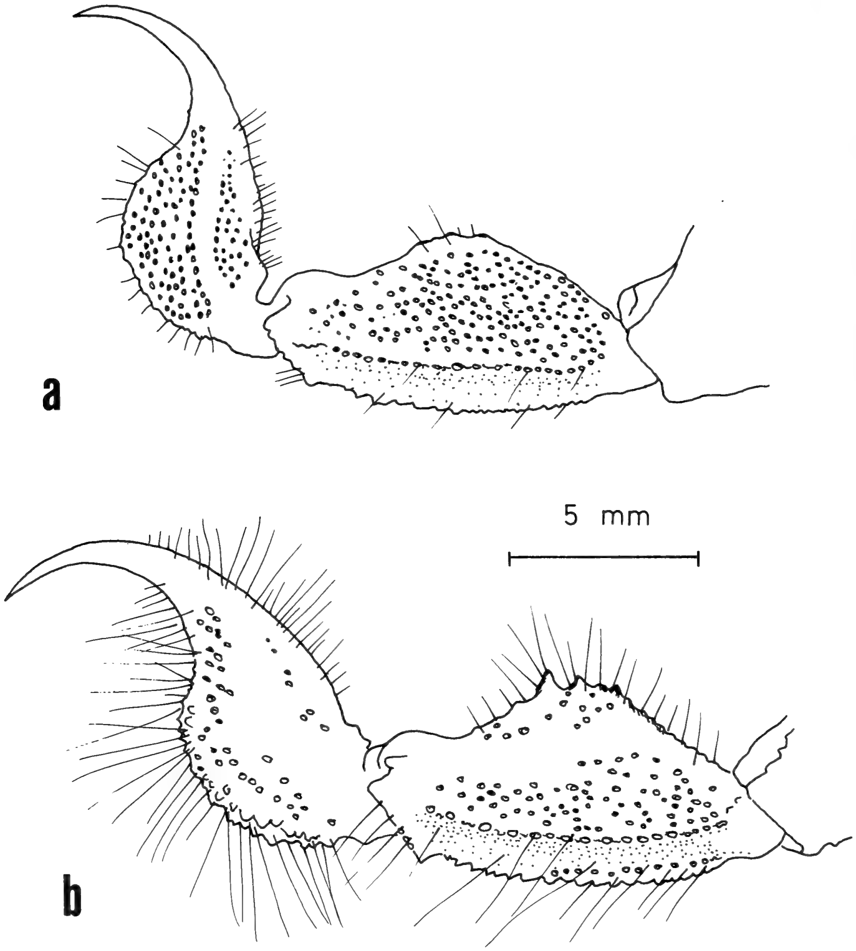

Fig. 6. Fifth caudal segment and telson of a. *Parabuthus capensis* (Ehrenberg) and b. *Parabuthus neglectus* Purcell.

as supports during this operation. To remove small stones or compacted soil the first two pairs of legs were tucked up under the body and the tail extended straight out backwards while the debris was transported rapidly backwards in a single movement, with the last two pairs of legs being used for traction. Only this latter part of the process is similar to the burrowing behaviour of *Opisthophthalmus*. The chelicerae were not observed to play any role in loosening the sand.

The distribution of *P. neglectus* extends from Clanwilliam northward to the Orange River, and eastward from De Doorns to Hanover and Graaff-Reinet in the west. This species appears to be randomly distributed in the desert and semi-desert regions of the Cape. In Namaqualand, the author has found this species in close association with *Opisthophthalmus granifrons* Pocock, and *Uroplectes carinatus* (Pocock).

P. neglectus also shows some colour variation. In northern Namaqualand specimens may have the last two caudal segments and telson darkly pigmented (Fig. 3b). This is also a feature of several other species in this area, *P. schlechteri* Purcell, *O. wahlbergi nigrovesicalis* Purcell and *O. w. gariepensis* Purcell.

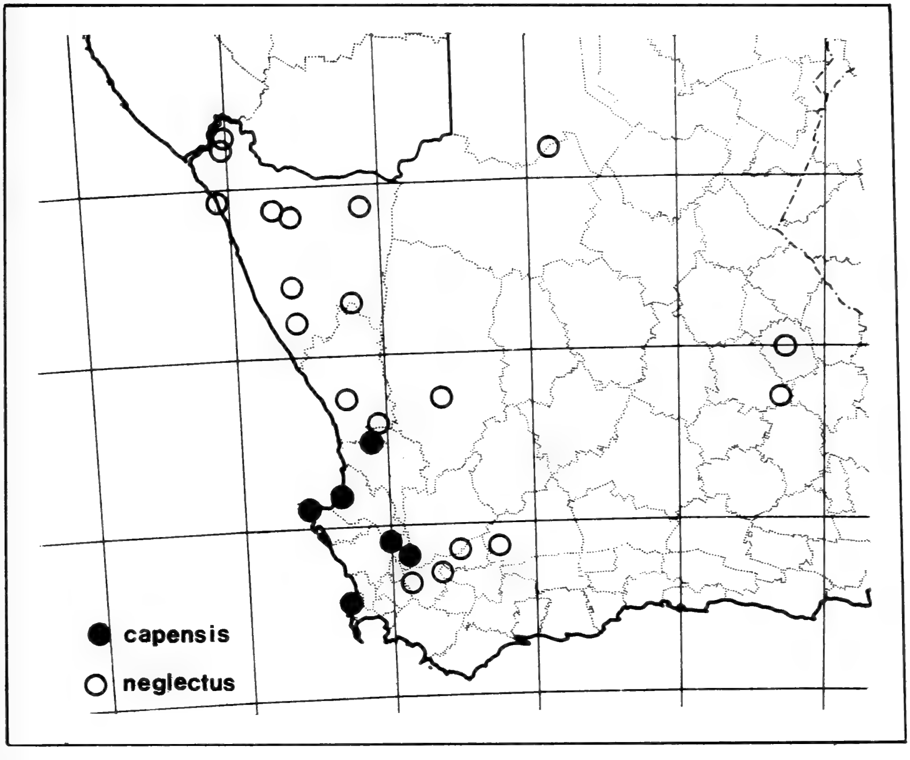

Fig. 7. Map showing distribution of the *Parabuthus capensis* species-group.

In the author's experience *P. capensis* has always been collected in areas of hard-packed soil, with the exception of the black specimens from Laaiplek, whereas *P. neglectus* has always been found in a sandy habitat. The longer and denser setae of *P. neglectus* indicates that this species is psammophilous, whereas the short and sparse setae of *P. capensis* indicates pelophily.

MATERIAL EXAMINED

All reference numbers refer to the South African Museum collection.

Parabuthus capensis (Ehrenberg) (yellow form)

Gouda (33°15′S 19°0′E)
1 ♀ (3758)

Tulbagh (33°20′S 10°10′E)
1 ♀ (504)

St Helena Bay (32°45′S 18°0′E)
3 ♂ ♂, 8 ♀ ♀ (10007, 11500, 12807)

Eendekuil (32°40′S 18°45′E)
2 ♀ ♀ (B8934)

Jacobsbaai (32°55′S 17°55′E)
1 ♂, 2 ♀ ♀ (C27)

Sak River
1 ♀ (B1753)

Hermanus (34°25′S 19°15′E)
2 ♂ ♂, 4 ♀ ♀ (11506)

Cape Peninsula (34°0′S 18°25′E)
1 ♂, 1 ♀ (12813, B545)

Parabuthus capensis (Ehrenberg) (black form)

Laaiplek (32°15′S 18°5′E)
2 ♂ ♂, 2 ♀ ♀ (C74)

Clanwilliam (32°5′S 18°50′E)
1 ♀ (C36)

Parabuthus neglectus Purcell

Clanwilliam (32°5′S 18°50′E)
5 ♂ ♂, 4 ♀ ♀ (3760, 1199, 3754)

Steinkopf (29°10′S 17°40′E)
4 ♂♂, 4 ♀♀ (567, 1704, 1711, 1713)

Concordia (29°30′S 18°0′E)
5 ♂♂, 5 ♀♀ (1702, 5198)

Garies (30°30′S 18°0′E)
5 ♂♂, 5 ♀♀ (1703, B7295, C43)

Okiep (29°35′S 18°0′E)
2 ♂♂, 3 ♀♀ (1701)

Aggenys (29°10′S 18°50′E)
1 ♂ (2948)

Port Nolloth (29°10′S 17°55′E)
1 ♀ (B568)

Kamieskroon (30°10′S 17°55′E)
6 ♂♂, 5 ♀♀ (B7314, B7338, C37)

Kliprand (30°30′S 18°40′E)
1 ♂ (C41)

Kuboos, Richtersveld (28°25′S 17°0′E)
8 ♂♂, 3 ♀♀ (B571, B8944)

Jakkalsputs, Richtersveld (28°35′S 17°0′E)
1 ♀ (C49)

Upington (28°30′S 21°15′E)
1 ♂, 1 ♀ (B8943)

Touws River (33°15′S 20°0′E)
3 ♀♀ (14263, 14365, 14378)

Van Rhynsdorp (31°35′S 18°40′E)
1 ♀ (1209)

Hanover (31°35′S 18°40′E)
1 ♂, 1 ♀ (9989, 9992)

Matjesfontein (33°15′S 20°35′E)
2 ♀♀ (12809, 14363)

Montagu (33°40′S 19°10′E)
1 ♀ (B3979)

De Doorns (33°30′S 19°40′E)
1 ♂ (B609)

Calvinia (31°30′S 19°50′E)
1 ♂ (12710)

Graaff-Reinet (31°30′S 24°30′E)
4 ♀ ♀ (12010)

ACKNOWLEDGEMENTS

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Purcell, W. F. 1902. On some South African Arachnida belonging to the Orders Scorpiones, Pedipalpi and Solifugae. *Ann. S. Afr. Mus.* **2**: 137–225.

ABBREVIATIONS

d	dorsals
db	dorsal basals
dt	dorsal terminals
e	externals
eb, Eb	external basals
esb, Esb	external suprabasals
est, Est	external subterminals
i	internals
it	internal terminals
V	ventrals
SAM	South African Museum, Cape Town
ZMB	Zoologisches Museum, Berlin

6. SYSTEMATIC papers must conform with the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae
Nuculana (*Lembulus*) *bicuspidata* (Gould, 1845)
Figs 14–15A

Nucula (*Leda*) *bicuspidata* Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (figs 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:
comma separates author's name and year
semicolon separates more than one reference by the same author
full stop separates references by different authors
figures of plates are enclosed in parentheses to distinguish them from text-figures
dash, not comma, separates consecutive numbers

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33°51′S 25°39′E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

7. SPECIAL HOUSE RULES

Capital initial letters

(a) The Figures, Maps and Tables of the paper when referred to in the text
e.g. '. . . the Figure depicting *C. namacolus* . . .'; '. . . in *C. namacolus* (Fig. 10) . . .'

(b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names
e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene

(c) Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as
'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

E. B. EASTWOOD

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PART 2

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VOLUME 73 PART 9 DECEMBER 1977 ISSN 0303-2515

ANNALS
OF THE SOUTH AFRICAN MUSEUM

CAPE TOWN

INSTRUCTIONS TO AUTHORS

1. **MATERIAL** should be original and not published elsewhere, in whole or in part.

2. **LAYOUT** should be as follows:

(a) *Centred masthead to consist of*
Title: informative but concise, without abbreviations and not including the names of new genera or species
Author's(s') name(s)
Address(es) of author(s) (institution where work was carried out)
Number of illustrations (figures, enumerated maps and tables, in this order)
(b) *Abstract* of not more than 200 words, intelligible to the reader without reference to the text
(c) *Table of contents* giving hierarchy of headings and subheadings
(d) *Introduction*
(e) *Subject-matter* of the paper, divided into sections to correspond with those given in table of contents
(f) *Summary*, if paper is lengthy
(g) *Acknowledgements*
(h) *References*
(i) *Abbreviations*, where these are numerous

3. **MANUSCRIPT**, to be submitted in triplicate, should be typewritten and neat, double spaced with 2,5 cm margins all round. First lines of paragraphs should be indented. Tables and a list of legends for illustrations should be typed separately, their positions indicated in the text. All pages should be numbered consecutively.

Major headings of the paper are centred capitals; first subheadings are shouldered small capitals; second subheadings are shouldered italics; third subheadings are indented, shouldered italics. Further subdivisions should be avoided, as also enumeration (never roman numerals) of headings and abbreviations.

Footnotes should be avoided unless they are short and essential.

Only generic and specific names should be underlined to indicate italics; all other marking up should be left to editor and publisher.

4. **ILLUSTRATIONS** should be reducible to a size not exceeding 12 × 18 cm (19 cm including legend); the reduction or enlargement required should be indicated; originals larger than 35 × 47 cm should not be submitted; photographs should be rectangular in shape and final size. A metric scale should appear with all illustrations, otherwise magnification or reduction should be given in the legend; if the latter, then the final reduction or enlargement should be taken into consideration.

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BULLOUGH, W. S. 1960. *Practical invertebrate anatomy.* 2nd ed. London: Macmillan.
FISCHER, P.-H. 1948. Données sur la résistance et de le vitalité des mollusques. *J. Conch., Paris* **88**: 100–140.
FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* **74**: 627–634.
KOHN, A. J. 1960*a*. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) **2**: 309–320.
KOHN, A. J. 1960*b*. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* **17** (4): 1–51.
THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. *In:* SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* **4**: 269–270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* **16**: 269–270.

(continued inside back cover)

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CRETACEOUS FAUNAS FROM ZULULAND, SOUTH AFRICA AND SOUTHERN MOZAMBIQUE THE APTIAN ANCYLOCERATIDAE (AMMONOIDEA)

By

HERBERT CHRISTIAN KLINGER
&
WILLIAM JAMES KENNEDY

Cape Town Kaapstad

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By

HERBERT CHRISTIAN KLINGER
South African Museum, Cape Town

&

WILLIAM JAMES KENNEDY
Geological Collections, University Museum, Oxford

(With 89 figures)

[*MS. accepted 14 April 1977*]

ABSTRACT

Heteromorph ammonites referred to the subfamilies Ancyloceratinae, Heteroceratinae, and Helicancylinae occur widely in rocks of Aptian age in northern Zululand and southern Mozambique. The subfamily Ancyloceratinae is represented by *Ancyloceras* (*Ancyloceras*), *Ancyloceras* (*Adouliceras*), *Tropaeum*, *Australiceras* and a specimen tentatively referred to *Lithancylus*. The subfamily Helicancylinae, separated from the Ancyloceratinae with some hesitation, is represented by *Toxoceratoides* and *Tonohamites* although doubt exists as to the generic affinity of some of the species. The subfamily Heteroceratinae is represented in the Upper Aptian by a helical hamitid-like form with or without tubercles, referred to a new genus, *Helicancyloceras*. Dimorphism is tentatively recognized in *Ancyloceras* (*Adouliceras*) and *Helicancyloceras*, whilst observations on the biogeography of the group are also included.

The following new species are described: *Ancyloceras* (*Adouliceras*) *cooperi* sp. nov., *Tropaeum dayi* sp. nov., *Tropaeum obesum* sp. nov., *Australiceras wandalina* (Boshoff MS) sp. nov., *Toxoceratoides? haughtoni* sp. nov., *Tonohamites? caseyi* sp. nov., *Helicancyloceras* (*Helicancyloceras*) *densecostatum* sp. nov., *Helicancyloceras* (*Nonyaniceras*) *nonyani* sp. nov., *Helicancyloceras* (*Nonyaniceras*) *circulare* sp. nov. and *Helicancyloceras* (*Nonyaniceras*) *crassetuberculatum* sp. nov.

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INTRODUCTION

Ammonites belonging to the family Ancyloceratidae are locally abundant in the Aptian of northern Zululand and southern Mozambique. Most specimens are fragmentary, and complete individuals rare, making positive identifications difficult in many instances. In the descriptions given below, the authors have in consequence made extensive use of open nomenclature in the sense of Richter (1948; see also Matthews 1973).

The family Ancyloceratidae is represented by the following subfamilies in the present collection: Ancyloceratinae Meek, 1876, Heteroceratinae Spath, 1922, and Helicancylinae Hyatt, 1900. Some of the Heteroceratinae have been described elsewhere (Klinger 1976).

The subfamilies of the Ancyloceratidae are all intimately related, and some may be superfluous; the authors retain them here as a working framework for classification of their material, for they do seem to show a reasonable degree of morphological homogeneity, and are of value when dealing with fragmentary material, as Thomson (1974: 17) has noted. Extensive splitting of the heteromorphs at family level, as suggested by Dimitrova (1970), is to be avoided in the authors' view, given the current state of knowledge of several groups which is still insufficient for a confident statement of their phyletic relationships, especially as many classic species require reinvestigation.

The Ancyloceratidae have a world-wide distribution and, following the systematic account, the authors give details of the palaeobiogeography of the group.

Generic comparisons may be drawn on a global scale, but at specific level most of the taxa encountered in the literature appear of more limited distribution, and some are markedly endemic. A close relationship exists, however, between the Barremian and Aptian faunas of Zululand and southern Mozambique and those of the southern U.S.S.R. as shown below, and as noted recently by Förster (1975*a*: 256, 1975*b*: 270).

The following species are described below:

Ancyloceras? sp. ind.
Ancyloceras? sp. cf. *humboldtiana* (Lea)
Ancyloceras (*Adouliceras?*) sp. cf. *ajax* Anderson
Ancyloceras (*Adouliceras*) *mozambiquense* (Krenkel)
Ancyloceras (*Adouliceras*) *cooperi* sp. nov.
Ancyloceras (*Adouliceras*) sp. gr. ex. *mozambiquense* (Krenkel)—*cooperi* sp. nov.
Lithancylus sp.
Tropaeum sp. aff. *subsimbirskense subsimbirskense* (Sinzow)
Tropaeum subsimbirskense compressum (Sinzow)
Tropaeum rossicum Casey
Tropaeum dayi sp. nov.
Tropaeum obesum sp. nov.

Tropaeum sp. aff. *undatum* Whitehouse
Tropaeum sp. gr. ex. *bowerbanki* J. de C. Sowerby *densistriatum* Casey—*hillsi* (J. de C. Sowerby)
Tropaeum sp. indet.
Australiceras ramososeptatum (Anthula)
Australiceras sp. aff. *irregulare* (Tenison Woods)
Australiceras wandalina (Boshoff MS) sp. nov.
Australiceras spp. indet.
Australiceras sp. cf. '*Crioceras*' *sarasini* Favre
Toxoceratoides royerianus (d'Orbigny)
Toxoceratoides krenkeli Förster
Toxoceratoides? haughtoni sp. nov.
Tonohamites koeneni Casey
Tonohamites sp. aff. *aequicingulatus* (von Koenen)
Tonohamites? caseyi sp. nov.
Helicancyloceras (*Helicancyloceras*) *vohimaranitraensis* (Collignon)
Helicancyloceras (*Helicancyloceras*) *densecostatum* sp. nov.
Helicancyloceras (*Helicancyloceras*) spp. indet.
Helicancyloceras (*Nonyaniceras*) *nonyani* sp. nov.
Helicancyloceras (*Nonyaniceras*) *circulare* sp. nov.
Helicancyloceras (*Nonyaniceras*) *crassetuberculatum* sp. nov.
Helicancyloceras (*Nonyaniceras*) spp. fragments
Incertae sedis.

LOCATION OF SPECIMENS

The following abbreviations are used to indicate the source of the material:

SAS	Geological Survey of South Africa, Pretoria
SAM	South African Museum, Cape Town
UPG	Department of Geology, University of Pretoria
BM(NH)	British Museum (Natural History), London
NMB	National Museum, Bloemfontein
OUM	University Musem, Oxford
UP	Palaeontological Institute, Uppsala University
MNHP	Muséum d'Histoire Naturelle, Paris.

FIELD LOCALITIES

Details of field localities referred to in this paper are given by Kennedy & Klinger (1975). Co-ordinates of additional localities in Zululand studied since then, and localities in southern Mozambique collected by M. R. Cooper are provided in the text.

MEASUREMENTS

Dimensions of specimens are given in millimetres; abbreviations are as follows:

D = diameter, Wb = whorl breadth, Wh = whorl height, U = umbilical diameter.

Figures in parentheses are dimensions expressed as a percentage of the total diameter. As no standard set of abbreviations for heteromorph ammonoids has as yet come into common use, other dimensions are written out in full.

SYSTEMATIC PALAEONTOLOGY

Class	CEPHALOPODA Zittel, 1884
Order	AMMONOIDEA Zittel, 1884
Suborder	ANCYLOCERATINA Wiedmann, 1966
Superfamily	ANCYLOCERATACEAE Meek, 1876
Family	**Ancyloceratidae** Meek, 1876
Subfamily	Ancyloceratinae Meek, 1876.

The features which allow separation of the Ancyloceratinae and Crioceratitinae are very slight indeed. Casey (1960) accorded the Ancyloceratinae and Crioceratitinae subfamilial rank. His extensive researches on the heteromorphs of the English Lower Greensand (Aptian to Lower Albian) have contributed enormously to our knowledge of these ammonites, and without his work the description of the Zululand and Mozambique species would have been rendered much more difficult. In view of this, the subfamilies are separated here also, although the differences in features which allow their distinction are slight.

The Ancyloceratinae are not well represented in the Cretaceous of Zululand and southern Mozambique, but few other ammonite groups present in the area grow to such enormous sizes and show such distinctive and bizarre coiling.

The subfamily is represented by the following genera: *Ancyloceras* s.l. d'Orbigny, 1842, *Tropaeum* J. de C. Sowerby, 1837, *Australiceras* Whitehouse, 1926, and *Lithancylus* Casey, 1960.

Genus *Ancyloceras* d'Orbigny, 1842

Type species

Ancyloceras matheronianum d'Orbigny, 1842 from the Lower Aptian of France by the subsequent designation of Haug (1889: 212).

Diagnosis

Small to large heteromorphs with ancyloceratid coiling; early whorls in contact or widely separated. Ornament consists of trituberculate ribs separated by a variable number of intermediate non-tuberculate ribs throughout, or only in early and late growth stages.

Subgenus *Ancyloceras* (*Ancyloceras*) d'Orbigny, 1842

Diagnosis

Ancyloceras in which trituberculate ribs are present throughout ontogeny.

Discussion

The genus *Ancyloceras* has become a receptacle for many heteromorphs showing ancyloceratid coiling, and as Casey (1960: 21) indicated, most of the Georgian (Gruzinian) ancyloceratids described by Rouchadzé (1933) are generically distinct from *Ancyloceras* and should probably be referred to *Pedioceras* or some genus within the Pedioceratinae. The same holds true for some ancyloceratid forms from the U.S.S.R. and from Bulgaria described by Drushchitz & Kudryavtsev (1960) and Dimitrova (1967) respectively. Inasmuch as the family Pedioceratidae is not well defined, and *Pedioceras* is a poorly-known genus (Yenne 1949 provides the most comprehensive discussion), it is perhaps wisest to retain the forms noted above in *Ancyloceras* with a mark of interrogation.

Ancyloceras (*Ancyloceras?*) sp. indet.

Figs 1A–B, 18B, 79D

Material

SAS H54/39 and SAS B11 from the Lower Aptian of Locality 170, Zululand.

Description

Only part of the initial coil and a non-septate fragment are known. Initial coiling appears to have been relatively close, with the whorls just touching, but not impressed. In SAS B11 (Fig. 1A–B) the two coils are not in one plane, but are helicoid. This does not appear to be due to postmortem damage. The whorl section is ovoid, wider than high (i.e. lateral diameter greater than siphonal–antisiphonal diameter) with a broadly rounded venter and dorsum. Ornament consists of major trituberculate ribs and a varying number (usually one to three) of intermediaries. The tubercles are very prominent and were originally spinose, and where the spines have broken off, low, round bosses remain, indicating the presence of a basal septum separating spine from shell.

The suture line is too poorly preserved for comment.

Dimensions

Specimen	*D*	*Wb*	*Wh*	*Wb/Wh*	*U*
SAS B11	*c.* 36	16,5(*c.* 49)	12,6(*c.* 20)	1,3	17(*c.* 47)

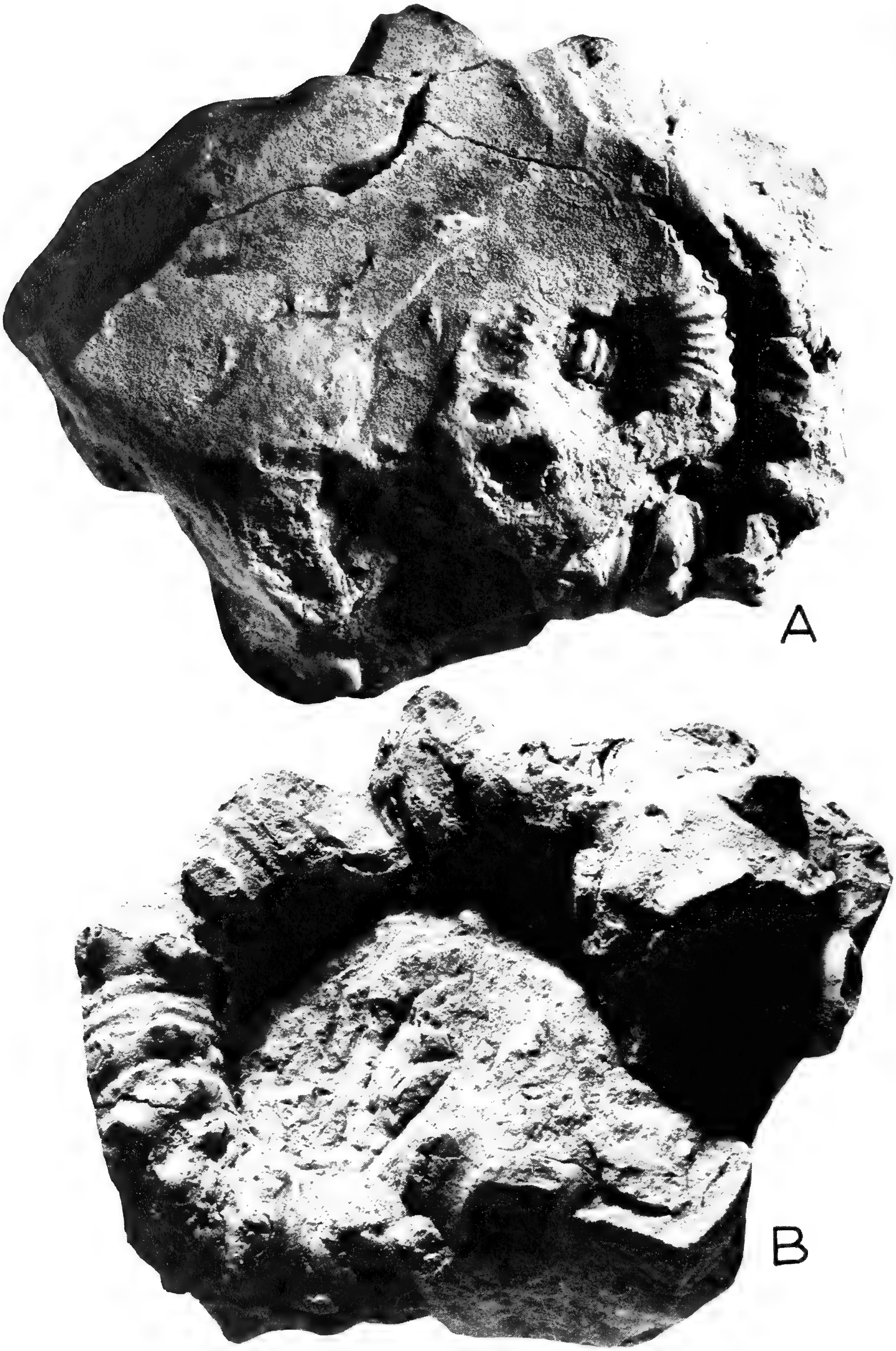


Fig. 1. A–B. *Ancyloceras* (*Ancyloceras?*) sp. indet. Dorsal and lateral views of specimen SAS B11 from locality 170, Aptian I. × 1,5.

Discussion

This is one of the few ammonites known in Bed 43 at locality 170 (see Kennedy & Klinger 1975, fig. 11). The fact that the coils in specimen SAS B11 are not in one plane, but rather appear helical, is disturbing. According to Clark (1958: 1076) the coiling in *Ancyloceras* is always planispiral, and is a feature (amongst others), which serves to distinguish *Ancyloceras* from *Anisoceras*. Unfortunately our material does not permit a more detailed investigation to determine whether coiling is helical throughout the species or merely restricted to this one specimen due to pathological reasons.

Ancyloceras helicoides Rouchadzè (1933: 217, pl. 8 (fig. 3)) from Kouthaïs, Georgia (U.S.S.R.) is a helically coiled ancyloceratid, and is referred to a new genus, *Kutatissites*, by Kakabadze (1970). If the Zululand species is indeed coiled helically in all specimens, it should be referred to *Kutatissites*. This would further accentuate the close similarity between the Lower Cretaceous faunas of the southern part of the U.S.S.R. and south-eastern Africa.

Until further material becomes known the authors prefer to retain the species in the genus *Ancyloceras* with a mark of interrogation.

Occurrence

Aptian I of Zululand.

Ancyloceras? sp. cf. *A. humboldtiana* (Lea, 1841)

Fig. 2

Compare:

Ancyloceras humboldtiana (Lea, 1841) *in* Forbes 1845: 171–172.

Material

BMNH C79717 from locality 166, Mfongozi Creek, Zululand, Aptian III.

Description

The single specimen consists of a fragment of the inner whorls and part of the outer whorl and straight shaft.

The inner whorl is ornamented by single, trituberculate ribs. On the outer whorl and shaft ribbing becomes sparse, and tuberculation weakened and possibly disappears. On the shaft the ribs are widely spaced with smooth interspaces.

Discussion

Obviously specific identification based on this fragment alone is impossible. The Zululand specimen bears some similarity to the specimen figured by Forbes, in possessing widely-spaced ribs on the shaft, but differs in lacking the fine intermediary ribs.

Fig. 2. *Ancyloceras?* sp. cf. *A. humboldtiana* (Lea, 1841). BMNH C79717 from locality 166, Aptian III. × 1.

Occurence

Upper Aptian of Zululand.

Subgenus *Ancyloceras* (*Adouliceras*) Thomel, 1964

Type species

Ancyloceras adouli Astier, 1851 by the original designation of Thomel (1964: 56).

Diagnosis

Coiling ancyloceratid, generally with small initial spire, the whorls of which expand rapidly. Tubercles are linked by two or three ribs, but disappear at varying diameters on the initial spire. Shaft generally ornamented by fine, dense ribs only, *without tubercles or differentiation into strong and weak ribs* for at least part of the length.

The crozier may be inflated and is generally ornamented by three strong rows of tubercles (lateral, lower and upper ventro-lateral) at some stage.

Discussion

Adouliceras was erected as a subgenus of *Ancyloceras* by Thomel (1964: 55) with *Ancyloceras adouli* Astier, 1851 as type species. The holotype, BMNH C73806, reposited in the British Museum (Natural History), is here illustrated as Figures 3–4. Thomel's original diagnosis is as follows:

> 'Le sous-genre *Adouliceras*, créé pour les formes du groupe d'*Ancyloceras adouli* ASTIER, est caractérisé par une *spire à croissance très rapide*, à cette partie de la coquille, un port remarquable. L'ornamentation de la spire est également particulière; elle consiste en côtes fines, simples toutes semblables, sur lesquelles on observe, de place en place, des tubercles, plus ou moins volumineux *à cheval sur deux ou trois consécutives*. La hampe, de section elliptique, est ornée de côtes simples, obliques, vigoureuses, généralement dépourvues de tubercules, du moins sur la partie cloisonnée. La crosse est connue seulement chez *A. adouli* ou elle porte des tubercules très vigoureux, et chez *A. renauxianum*.'

In addition to the type species, *A. kaliae* (Sarkar), *A. collignoni* (Sarkar) and *A. renauxianum* were referred to the subgenus. Comparison of *A. adouli* and *A. renauxianum* shows the extreme variation encountered in *A.* (*Adouliceras*). In *A.* (*Ad.*) *adouli* the whorl section becomes abruptly inflated towards the hook. Furthermore, the initial spirally coiled section in the latter lacks tuberculation altogether. (See d'Orbigny 1842, pl. 123.) Whether this is in fact true, or merely another of d'Orbigny's artist's restorations is unknown.

Recently Murphy (1975) described a species from California under the name of *Ancyloceras thomeli*. In all respects this species has the characteristics of *Adouliceras*, apart from the fact that 'the spire of *A. thomeli* tapers much less rapidly than that of *A. adouli* which, according to Thomel (personal communication) is grounds for excluding the California form from *Adouliceras*' (Murphy 1965: 25). Comparison of the holotype of *A.* (*Ad.*) *adouli*, Figures 3–4, with the specimen figured by Thomel (1964, pl. 9 (fig. 2)) shows that the size of the initial spire is variable. This is further borne out by the Zululand and Mozambique material to be described below. The presence or absence of fine ribs on the hook quoted by Murphy as being a reason for separating *Ancyloceras thomeli* from *A.* (*Ad.*) *adouli* is just as variable.

It is here proposed to consider the absence of tubercles or stronger ribbing on part of the shaft and the mode of ornament on the early whorls as constituting the main characteristic of *Adouliceras*. The size of the initial spire is generally smaller than that of *Ancyloceras* s.s.

Fig. 3. *Ancyloceras* (*Adouliceras*) *adouli* Astier, 1851. BMNH C73806, the original of Astier (1851, pl. 6 (no. 12), pl. 7 (no. 12 bis)), from the Neocomian of Cheiron, Basses Alpes (France). × 0,45.

Fig. 4. *Ancyloceras* (*Adouliceras*) *adouli* Astier, 1851. As in Figure 3.

In addition to the species mentioned above, the following may possibly also be referred to *Adouliceras: Ancyloceras attrox* Anderson (1938: 209 pl. 69 (figs 1–3)) and *Ancyloceras ajax* Anderson (1938: 210, pl. 65 (figs 1–3)). *Ancyloceras ewaldi* Dames (1880: 690, pl. 25, pl. 26 (fig. 1)) is probably also an example of *Adouliceras.*

Adouliceras represents a line of development which resembles that of *Australiceras* gr. ex. *gigas*, and some species were previously referred to that genus (e.g. Casey 1961: 51). Thomel (1964: 60, table 2), however, has shown that they are parallel but apparently unrelated lineages.

Adouliceras differs from *Ancyloceras* s.s. in lacking tubercles on part of the shaft. It differs from *Australiceras* gr. ex. *gigas* mainly in having a smaller initial spire, a different mode of tuberculation, looser coiling, and, most important of all, in lacking major costae and tubercles on the shaft. It may be distinguished from uncoiled species of *Tropaeum* e.g. *T.* gr. ex. *hillsi* by the possession of three rows of tubercles on the early and late parts of the shell. Non-tuberculate fragments of the ammonitic coils are generically indistinguishable from *Tropaeum.*

Unfortunately the South African and Mozambique material does not shed any light on the phylogeny and relationship of *Adouliceras* to other genera of the Ancyloceratinae.

Occurrence

Upper Barremian and Lower Aptian of western and central Europe, California, Zululand and Mozambique.

Ancyloceras (*Adouliceras?*) sp. cf. *ajax* Anderson, 1938

Figs 5–6A

Compare:

Ancyloceras ajax Anderson, 1938: 210, pl. 65 (figs 1–3).

Material

SAS Zo(1) from locality 162, Mfongozi Creek, Zululand. Lower ? Aptian.

Description

One large fragment consisting of the non-septate part of the shaft and crozier is compared to Anderson's species. The terminal septum is exposed at the broken end of the shaft.

The section of the shaft is ovoid, with a greater dorso-ventral than lateral diameter. Towards the crozier the whorl breadth increases rapidly, surpassing the whorl height. On the recurved end the whorl section is depressed with a flattened dorsum, moderately angular umbilical edge, and a broadly rounded venter.

Ornament on the shaft consists of low, rounded, oblique, prorsiradiate ribs. The ribs cross the dorsum with a slight forward curvature. The venter is abraded,

Fig. 5. *Ancyloceras* (*Adouliceras*) sp. cf. *ajax* Anderson, 1938. SAS Zo(n) from locality 162, Mfongozi Creek, Zululand, Lower? Aptian. × 0,4.

but it appears that the ribs crossed the venter without diminution. There are about 25 ribs in a distance equal to the whorl height. At a point 70–80 mm before the bend in the crozier, strong ribs appear, becoming progressively stronger towards the bend. Umbilical, lateral and ventral tubercles develop on the major ribs. The major ribs cross the flanks radially and curve forward over the venter, but are effaced on the dorsum.

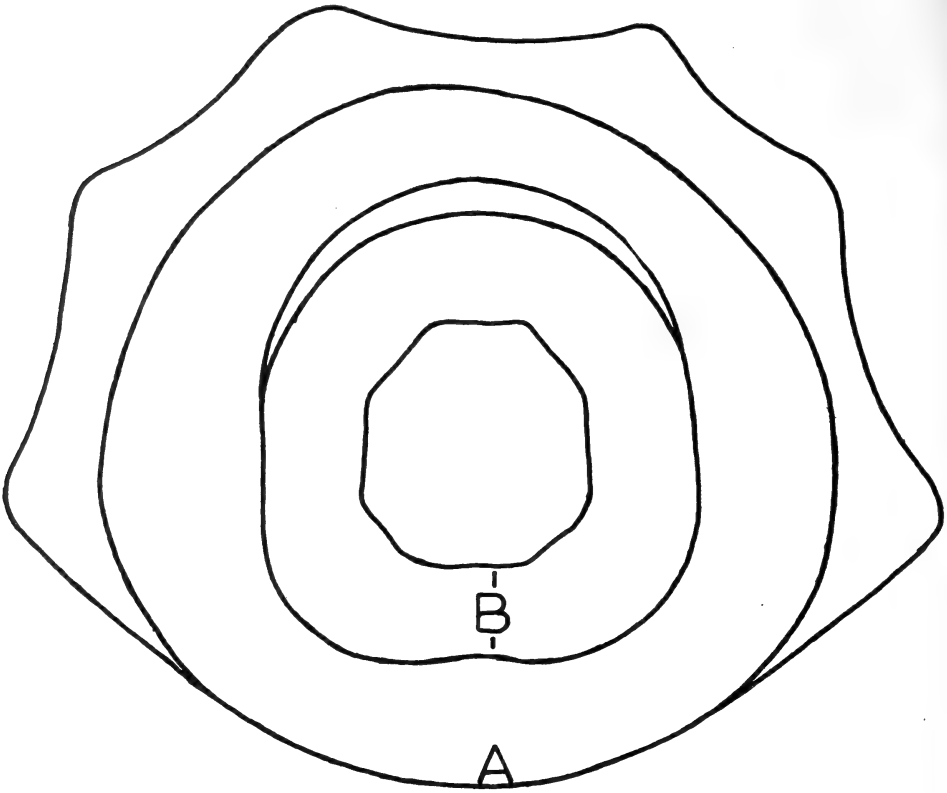


Fig. 6. A. Whorl section of *A.* (*Adouliceras*) sp. cf. *ajax* Anderson, 1938. SAS Zo(n). × 1. B. Whorl section of *Australiceras wandalina* sp. nov. UPG B8 from Manyola Drift, Aptian III. × 0,5.

Dimensions

Wb	80	101,5	89,5
Wh	92,5	91,6	97,0
	End of shaft.	In crozier.	Aperture.

Discussion

The specimen bears a strong resemblance to the Californian *Ancyloceras ajax*, but lacks the inflated body chamber and the very strong tuberculation on the crozier.

Ancyloceras thomeli Murphy (1975: 24, pl. 3 (figs 1, 5), pl. 11 (figs 1–2)) also differs on account of the presence of an inflated body chamber.

In *A.* (*Ad.*) *renauxianum* d'Orbigny (1842: 499, pl. 123) non-tuberculate intermediaries occur between the major costae in the crozier. *A.* (*Ad.*) *ewaldi* Dames (1880: 690, pl. 25, pl. 26 (fig. 1)) has stouter ribbing on the shaft, and more closely spaced ribs on the crozier. *A.* (*Ad.*) *adouli* Astier (1851: 23, pl. 6 (nr 12); pl. 7 (nr 12b); see also Thomel 1964, pl. 9 (fig. 2)) has a strongly inflated body chamber and is readily distinguishable from the present specimen.

Occurrence

The exact stratigraphic position of the Zululand specimen is unknown, although definitely Aptian. Anderson's species is said to come from close to the Barremian/Aptian boundary.

Ancyloceras (*Adouliceras*) spp.

group of *mozambiquense* Krenkel—*cooperi* nov.

Abundant leached concretions yielding fragments of ancyloceratids litter the surface and topsoil at locality 170. The stratigraphic interval represented by these concretions is at least 10 m, whilst similar material from Da Silva's (1962) locality A (26°49′50″S 32°12′55″E) herein referred to as Lubemba, in southern Mozambique is available. Apart from the ancyloceratids, the associating fauna consisting of *Cheloniceras* spp., *Neosilesites* and *Valdedorsella* indicates a Lower Aptian age in both cases, and subsequent work by Förster (1975*a*) confirms this.

All the ancyloceratid fragments consist either of parts of the early whorls, parts of the uncoiled shafts and/or the crozier, and at the time of writing, no complete specimen has been found. Two different kinds of early whorls can be identified; one with a circular, the other with a subtrigonal whorl section, the latter type being commonest. The shaft and croziers, on the other hand are so varied that hardly two specimens are alike. In addition to differences in ornamentation, remarkable differences in size occur, Macro- and micro-conchs being present.

The early whorls with subtrigonal whorl section can be identified with *A.* (*Ad.*) *mozambiquense* Krenkel; those with circular whorl section are referred to a new species, *A.* (*Ad.*) *cooperi* sp. nov. Some types of shaft and crozier may tentatively be referred to the two species. However, due to the extreme variability, and the absence of any complete specimens for definite allocation, the shafts and croziers are referred in open nomenclature to *A.* (*Ad.*) gr. ex. *mozambiquense—cooperi*. Admittedly, this may be interpreted as vertical systematics *par excellence*, but in the authors' opinion this is preferable to the other alternatives—to ignore the material until such time as future collecting may hopefully yield a complete specimen, or to erect a number of species based on incomplete specimens as has so often been done in the past. Moreover, identification based on the shaft and crozier alone is impracticable as will be shown in the discussion below, for even unrelated groups of heteromorphs may have the same type of crozier.

Ancyloceras (*Adouliceras*) *mozambiquense* Krenkel, 1910

Figs 7, 8A–B, 9B, 10B, 11B, 12A, D

Ancyloceras sp. Kilian, 1902: 465.
Ancyloceras fallauxi Uhl. n. var. *mozambiquense* Krenkel, 1910: 153, pl. 17 (figs 2–3).
? *Ancyloceras fallauxi* Uhlig var. *mozambiquense:* Haughton & Boshoff, 1956: 14.
Tropaeum mozambiquense: Wachendorf, 1967: 292, pl. 34 (fig. 1). *Non* Da Silva 1962: 21, pl. 9 (figs 1–2), pl. 10 (fig. 1), pl. 11 (fig. 1), pl. 12 (fig. 1), pl. 13 (fig. 1), pl. 14 (fig. 1).
? *Tropaeum* cf. *hillsi:* Förster, 1975*a*: 151, pl. 2 (fig. 1), text-fig. 28.
Australiceras mozambiquense: Förster, 1975*a*: 155, pl. 3 (fig. 3), text-fig. 31.

Holotype

The specimen figured by Krenkel (1910, pl. 17 (figs 2–3)) reported to have been collected from near Delagoa Bay, Mozambique.

Neotype

SAM–PCM5349 (Fig. 7) from Lubemba, southern Mozambique. The holotype was destroyed by bombing during 1944.

Material

SAM–PCM5314, SAM–PCM5351, SAM–PCM5438 from Lubemba, southern Mozambique; SAS 54/45; SAS 54/41/4; SAS 54/45/2; BMNH C78883 and BMNH C78884 from locality 170, Mlambongwenya Creek, Zululand. Aptian I–II.

Description

Coiling is crioceratitid but very variable. On the most complete specimen, SAM–PCM5349 (Fig. 7), the inner whorl is not in contact with the outer. Some specimens, however, have a distinct dorsal impression of the ventral tubercles on the preceding whorl. The whorl section is typically subtrigonal to rectangular, higher than wide with a flattened but not impressed dorsum and slightly inflated flanks converging to a moderately rounded venter. In some specimens the dorsum is rounded and convex (Fig. 8A).

As can be seen from the impression of the inner whorl of specimen SAM–PCM5349 (Fig. 7), juvenile ornament consists of very fine, radial ribs which cross the dorsum with traces of duplication. The umbilical tubercles appear to be most prominent, and appear as low, rounded bosses, covering one to three ribs. The bosses probably indicate the former presence of long spines, with a basal septum. The lateral tubercles are smaller and more pointed. Ventral tubercles are not preserved, but judging by their impression on the dorsae of some of the larger whorls, were quite prominent and situated close to each other on either side of the siphonal line.

At larger diameters, ribbing becomes weaker and curves forward over the dorsum, although radial to slightly sinusoidal across the flanks. The ribs cross the venter without visible sign of interruption. Bifurcation of ribbing occurs at the umbilical edge, or on the dorsal third of the flanks. The diameter at which tuberculation disappears is very variable, the ventral and lateral tubercles disappearing first. At a whorl height of approximately 45 mm, the last umbilical tubercles are visible. There are about 11 to 13 ribs in a distance equal to the whorl height.

The suture is highly incised and dendritic. Unfortunately, however, none of the specimens is suitable for reproduction of the whole suture line.

Fig. 7. *Ancyloceras* (*Adouliceras*) *mozambiquense* Krenkel, 1910. SAM–PCM5349, neotype from the Lower Aptian of Lubemba, Mozambique. Collected by M. R. Cooper. × 1,3.

Fig. 8. *Ancyloceras* (*Adouliceras*) *mozambiquense* Krenkel, 1910. A. SAS 54/45. B. SAS 54/1. Both from the Lower Aptian, Aptian I–II of locality 170. × 1.

Fig. 9. A. *Ancyloceras* (*Adouliceras*) gr. ex *mozambiquense-cooperi*. SAM–PCM5328, crozier from the Lower Aptian of Lubemba, Mozambique. Note the strong development of the umbilical and lateral tubercles. × 0,85. B. *Ancyloceras* (*Adouliceras*) *mozambiquense* Krenkel, 1910. SAS 54/45/2 from locality 170, Zululand, Lower Aptian, Aptian I–II. × 1.

Fig. 10. A. *Australiceras?* sp. cf. '*Crioceras*' *sarasini* Favre, 1908. SAS H71D/18 from Nhlohlela pan, Mkuze Game Reserve, Zululand, Aptian III–IV. × 1. B. *Ancyloceras* (*Adouliceras*) *mozambiquense*. SAS 54/45 from locality 170, Zululand, Aptian I–II. × 1,2.

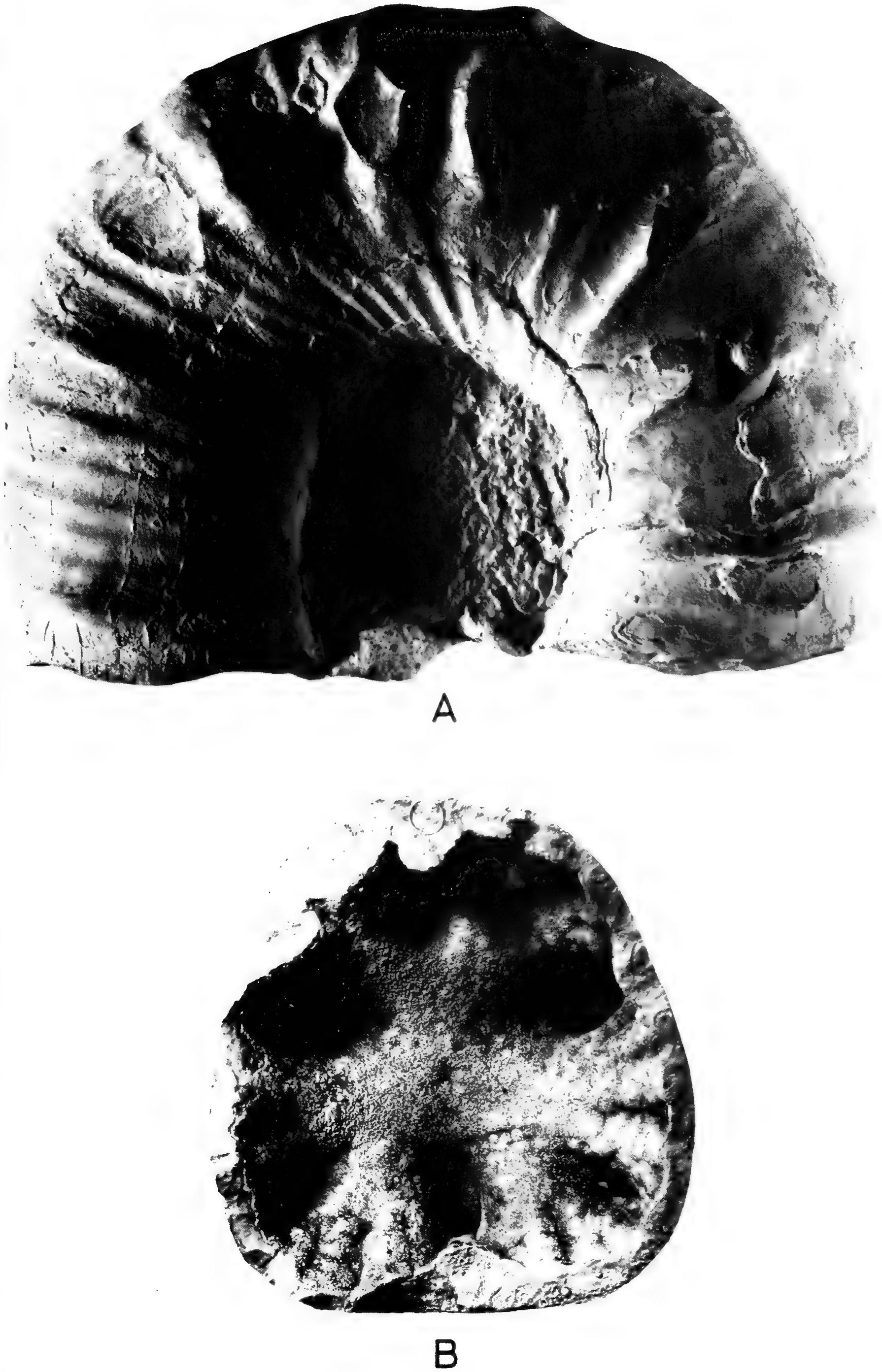


Fig. 11. A. *Ancyloceras* (*Adouliceras*) gr. ex *mozambiquense-cooperi*. SAS 54/45/3, crozier from locality 170, Zululand, Aptian I–II. Form 3 with only laterally developed tubercles in crozier. × 0,54. B. *Ancyloceras* (*Adouliceras*) *mozambiquense* Krenkel, 1910. SAS 54/41/3 from locality 170, Zululand, Aptian I–II. × 1,2.

Dimensions

Specimen	*Wb*	*Wh*	*Wb/Wh*
SAM-PCM5349	44	47	0,93
SAS 54/41/3	51,6	56,4	0,91

Discussion

It is difficult to understand how Krenkel's (1910: 153) original description of the species was so consistently misinterpreted by subsequent workers; Krenkel states of the unique holotype (destroyed during the Second World War):

> '. . . das aus dem Übergang des spiral eingerollten Teiles zum Schaft stammt. Die Innenseite zeigt keine Spur einer Berührung mit dem früheren Umgange.'

Da Silva's interpretation of Krenkel's species is unacceptable, and his *Tropaeum mozambiquense* was merely a catch-all for fragments of a variety of *Tropaeum*. The specimen which Da Silva (1962: 21, pl. 9, figs 1–2) described as corresponding to Krenkel's original, has a distinctly impressed dorsal zone, and this is a feature Krenkel explicitly stated to be absent. Förster (1975*a*) has recently described material from the same area in Mozambique, and he realized that most of Da Silva's specimens of '*Tropaeum mozambiquense*' were better referred to *Tropaeum subsimbirskense compressum* (Sinzow). Förster also noted the presence of three rows of tubercles on some of his material and concluded that Krenkel's species must be an australiceratid, with affinities with *A. rabenjanaharyi* Collignon and *A. ramososeptatum* (Anthula), again a departure from Krenkel's original concept.

Other finely ribbed species of *Tropaeum* bear a strong similarity to the non-tuberculate fragments of *A.* (*Ad.*) *mozambiquense*. On the basis of the present material, however, the ancyloceratid character of the species is firmly established.

A. (*Ad.*) *mozambiquense* is easily distinguished from other species of *A.* (*Adouliceras*) by the sub-triangular whorl section and by the relatively large planispirally coiled immature stage which is a departure from the normal *Adouliceras* pattern.

Occurrence

Lower Aptian, Aptian I–II of Zululand and southern Mozambique.

Ancyloceras* (*Adouliceras*) *cooperi sp. nov.

Figs 12B–C, 13A–C, 14A–C

Holotype

SAM-PCM5317 in the South African Museum, from Lubemba, southern Mozambique. Collected by M. Cooper. Aptian I–II.

Derivation of name

The species is named for Michael Cooper, of Wolfson College, Oxford, who collected the type material.

Material

Apart from the holotype; SAM–PCM5313, SAM–PCM5215, from Lubemba, and SAS 54/41/1 and SAS 54/41/2 from locality 170, Mlambongwenya, Zululand, Aptian I–II.

Description

Coiling is tight, resulting in a small planispirally coiled section. The whorls, however, are not impressed. The very early whorls are unknown, but at a diameter of *c*. 20 mm the section is already essentially circular, and only a little wider than high. The dorsum is slightly flattened, but with no trace of the impressed zone. Ornament initially consists of radial, single, broad, low ribs, each bearing three rows of low and rounded tubercles. The tubercles are of approximately equal size, and appear to be the bases of septate spines. The tuberculate ribs are separated by one or two narrow intermediaries. The latter are thin and separated by interspaces of equal width. They sweep backward over the umbilical wall, and are straight and radial to rursiradiate across the flanks and pass straight across the venter. On the dorsum, the ribs curve forward and show a notable tendency towards duplication. With increasing diameter the major ribs tend to become wider and the lateral and ventral tubercles disappear at a whorl breadth of around 23 mm. At this stage, ribs now arise in two's, three's and four's from the remaining, but weakened, umbilical tubercles. On the holotype, umbilical tubercles are still visible at a whorl breadth of 32 mm, but on another specimen, SAS 54/41/2 (Fig. 14), no sign of tubercles is visible at a whorl breadth of 21 mm. Two very slight constrictions are present on SAM–PCM5313.

Dimensions

Specimen	*D*	*Wb*	*Wh*	*Wb/Wh*	*U*
SAM–PCM5317	89,2	37(41,4)	40,2(45)	0,92	33,5(37,5)

Discussion

The round whorl section clearly distinguishes *A.* (*Ad.*) *cooperi* from *A.* (*Ad.*) *mozambiquense*. Furthermore, the initial spire is much smaller in the former. The holotype bears a superficial resemblance to some of the species redescribed by Thomel (1964), e.g. *A.* (*Ad.*) aff. *collignoni* Sarkar, 1955 (Thomel 1964: 58, pl. 9 (fig. 1), text-fig. 7A), *A.* (*Ad.*) *kaliae* Sarkar 1955 (Thomel 1964: 57, pl. 10 (fig. 1), text-fig. 7B), and *A.* (*Ad.*) *adouli* Astier (Thomel 1964: 56, pl. 9 (fig. 2), text-fig. 7C) as far as the size of the planispirally coiled section is concerned. *A.* (*Ad.*) *adouli* has a whorl section similar to that of the present species, but lacks the regular tuberculation (see Thomel 1964: 58, fig. 7) and has

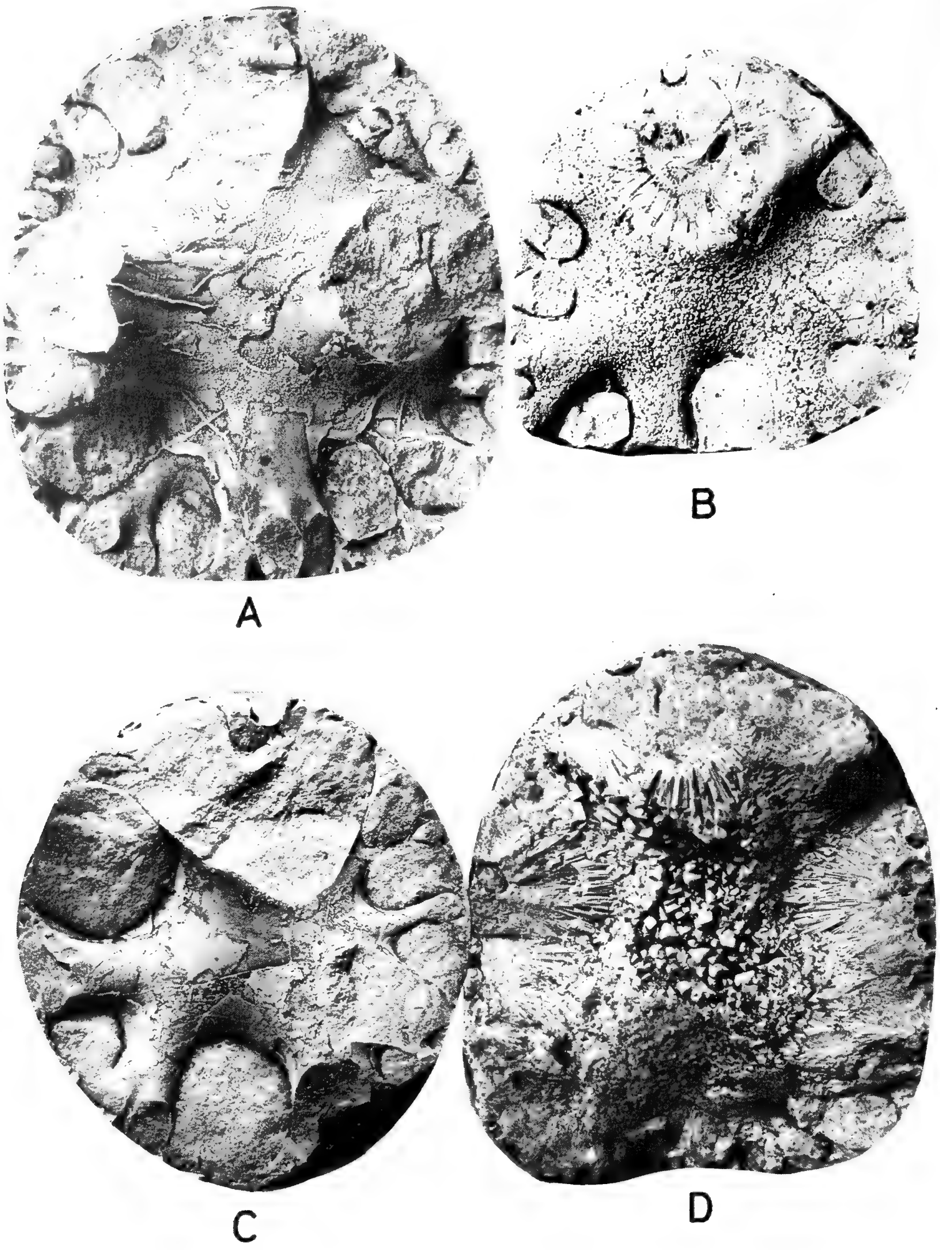


Fig. 12. A. *Ancyloceras* (*Adouliceras*) *mozambiquense* Krenkel, 1910. SAM–PCM5505 from Lubemba, Mozambique, Lower Aptian. × 1,3. B. *Ancyloceras* (*Adouliceras*) *cooperi* sp. nov. SAM–PCM5215 from same locality and horizon as above. × 1,4. C. *Ancyloceras* (*Adouliceras*) *cooperi* sp. nov. SAS 54/42/2 from locality 170, Zululand, Aptian I–II. Typical rounded form. × 1,4. D. *Ancyloceras* (*Adouliceras*) *mozambiquense* Krenkel, 1910. SAM–PCM5351 from Mozambique, Lower Aptian. × 1,3.

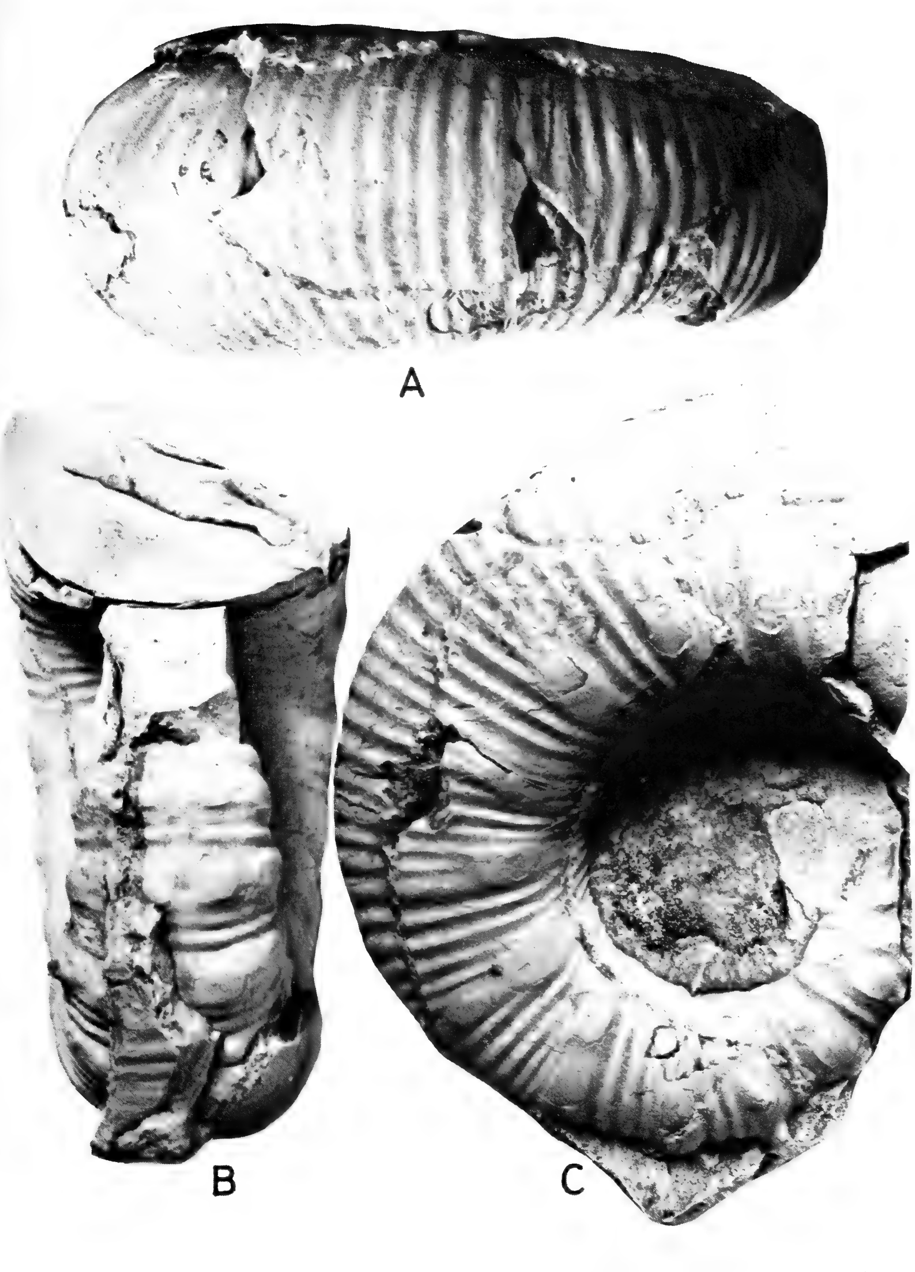


Fig. 13. A–C. *Ancyloceras* (*Adouliceras*) *cooperi* sp. nov. SAM–PCM5317, holotype from Lubemba, Mozambique, Lower Aptian. × 1,05.

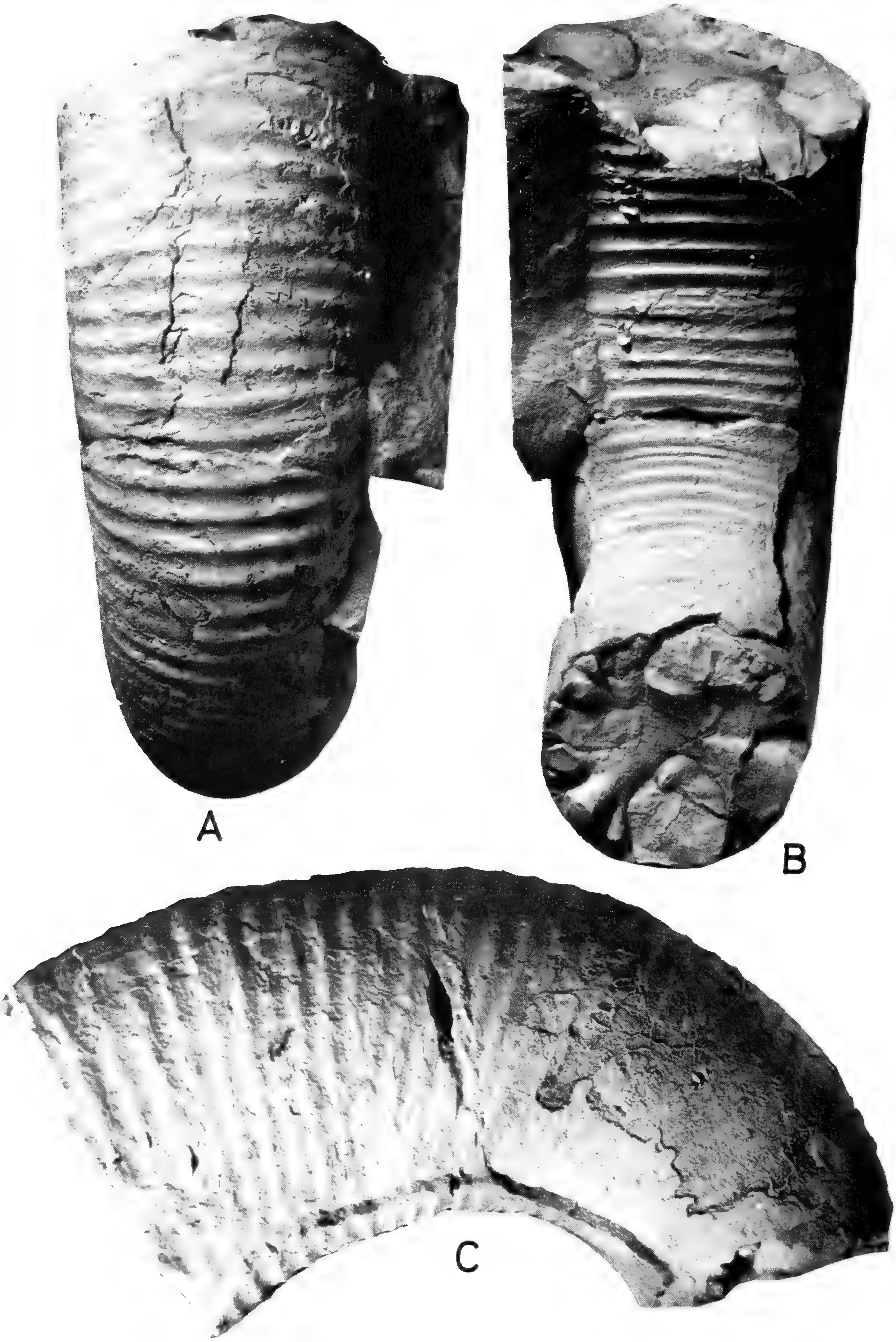


Fig. 14. A–C. *Ancyloceras* (*Adouliceras*) *cooperi* sp. nov. SAS 54/41/2 from locality 170, Zululand, Aptian I–II. × 1.

numerous intermediary ribs. *A.* (*Ad.*) *kaliae* Sarkar from the Upper Barremian is very similar as far as ornamentation is concerned, but has an ovoid whorl section. *A.* (*Ad.*) aff. *collignoni* has irregular ornamentation.

Occurrence

Lower Aptian of Zululand and Mozambique.

Ancyloceras (*Ad.*) gr. ex. *mozambiquense–cooperi*

(Description of shafts and croziers)

Form 1

Figs 15, 16, 17, 18A, 19, 20A–B

Material

SAM–PCM5337, SAM–PCM5395, SAM–PCM5368, SAM–PCM5449, SAM–PCM5324, from Lubemba, southern Mozambique. BMNH C7884 from Locality 170, Zululand.

Description

The shaft is of variable length with a subtrigonal section, having a narrower venter than dorsum and weakly inflated flanks. Towards the crozier the dorsum becomes more flattened and the dorso-ventral width increases. In the bend of the crozier and on the descending limb the whorl section is dome-shaped with a flat dorsum and broadly rounded flanks and venter. There is no distinct inflation of the body chamber.

At the proximal end of the shaft, ornament consists of narrow, low, slightly prorsiradiate ribs only, separated by wider interspaces. Average rib density is about sixteen to eighteen per dorso-ventral diameter. On the distal half to third of the shaft, stronger ribs start appearing on the flanks, bearing umbilical and lateral tubercles. These ribs and the tubercles become progressively more prominent towards the bend in the crozier. At the bend the intermediaries become fainter and eventually disappear. In the bend itself, one or two of the major costae now acquire ventral tubercles and cross the venter with a forward curvature. At this stage the lateral tubercles are generally strongest. In the descending limb the ribs become narrower and increasingly flared, accompanied by loss of tuberculation. Three flared ribs are present in the most complete specimen.

The last septum occurs at a point coinciding approximately with the onset of major ribbing.

Dimensions

Specimen	SAM–PCM5324	SAM–PCM5368
Wb. at proximal end of shaft . . .	91	78
Wh. at proximal end of shaft . . .	105	87
Wb. in crozier	117	99

Specimen	SAM–PCM5324	SAM–PCM5368
Wh. in crozier	109	93
Wb. near aperture	110	97
Wh. near aperture	100	90
Width of crozier = venter of shaft to venter of descending limb	295	230

Discussion

This is the most common form present, and it is likely that it belongs to the planispiral whorls identified as *A.* (*Ad.*) *mozambiquense*, which are also the most abundant, as is suggested by the subtrigonal whorl. Until more complete material becomes available to substantiate or discredit this assumption, it is considered advisable to refer the shafts and croziers in open nomenclature to *A.* (*Ad.*) gr. ex. *mozambiquense–cooperi.*

A number of shafts and croziers from various unrelated species with quite distinct early whorls are virtually identical to, or impossible to distinguish from, the group of specimens available. These include *A.* (*Ad.?*) *durelli* Anderson (1938: 210, pl. 65 (figs 1–2), pl. 68 (fig. 1)), *Ancyloceras matheronianum* d'Orbigny *in* Drushchitz & Kudryavtsev (1960, pl. 34 (fig. 2)), *Ancyloceras urbani* Neumayr & Uhlig, 1881, and *Ancyloceras rochi* Dimitrova (the latter two *in* Dimitrova 1967, pls 23, 24 respectively), and it is apparent that species based on croziers and shafts are of little value in at least some ancyloceratid genera.

Form 2

Fig. 21B

Description and discussion

Crozier SAS 54/45/5 is virtually identical to the previous form as far as ornamentation is concerned, but is only half the size. These differences probably reflect sexual dimorphism, although this has not been widely recognized in ancyloceratids.

Dimensions

Wb. at proximal end of shaft	54
Wh. at proximal end of shaft	66
Wb. in crozier	66
Wh. in crozier	—
Wb. near aperture	71
Wh. near aperture	67
Width of crozier	180

Form 3

Figs 11A, 23

Description and discussion

Crozier SAS 54/45/3 has only one lateral row of irregularly developed tubercles and does not develop flared ribbing immediately before the aperture.

Dimensions

Wb. at proximal end of shaft	—
Wh. at proximal end of shaft	78
Wb. in crozier	*c.* 91
Wh. in crozier	81
Wb. at aperture	92
Wh. at aperture	86
Width of crozier	215

Fig. 15. *Ancyloceras* (*Adoulticeras*) gr. ex *mozambiquense-cooperi*. SAM–PCM5324, crozier from Lubemba, Mozambique. Lower Aptian. Most common form, Form 1. × 0,48.

Fig. 16. *Ancyloceras* (*Adouliceras*) gr. ex *mozambiquense-cooperi*. SAM–PCM5324, ventral view of crozier from Lubemba, Mozambique, Lower Aptian. Most common form, Form 1. × 0,57.

Fig. 17. *Ancyloceras* (*Adouliceras*) gr. ex *mozambiquense-cooperi*. SAM–PCM5368, ventral view of crozier from Lubemba, Mozambique, Lower Aptian. Most common form, Form 1. × 0,67.

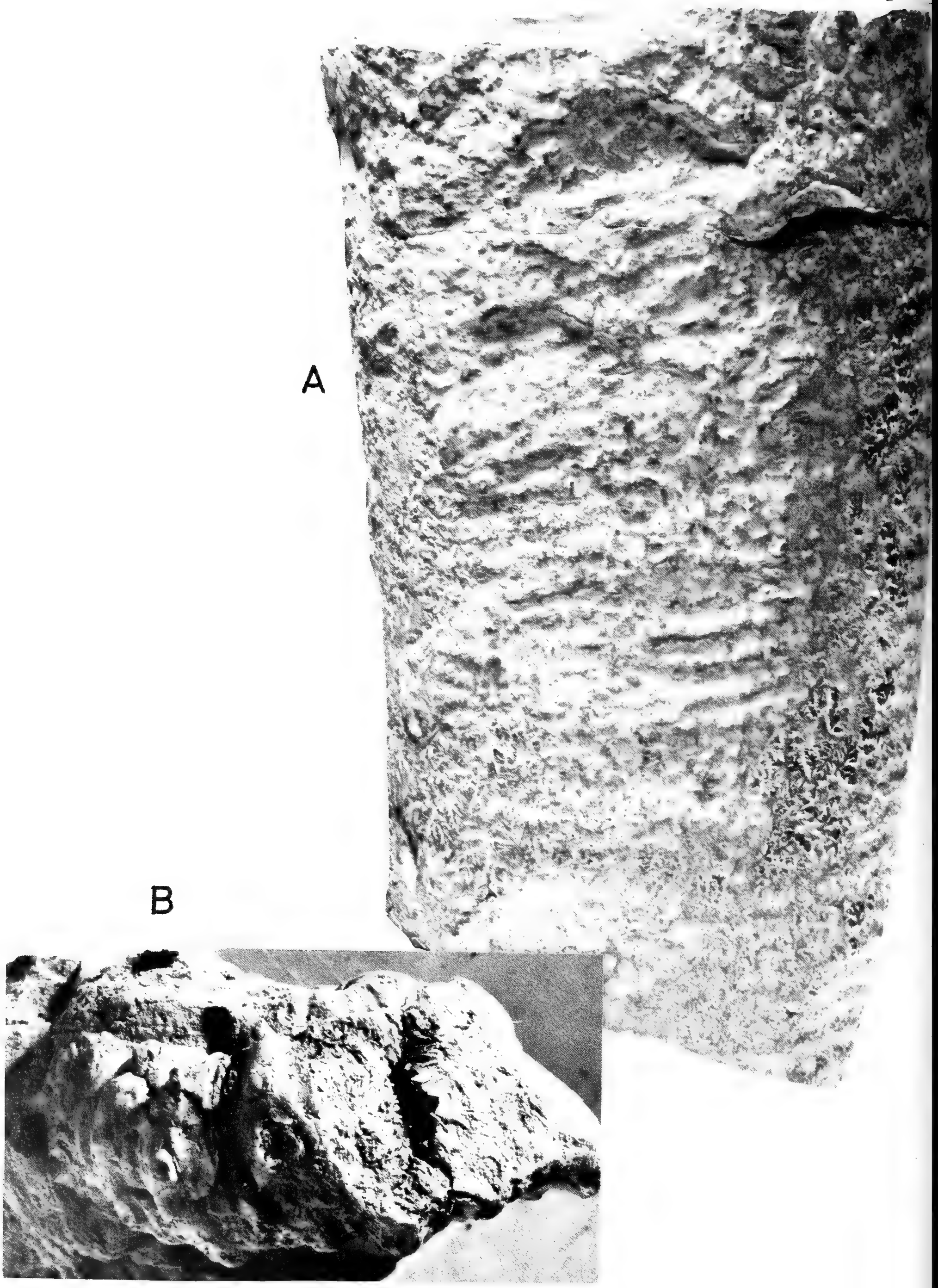


Fig. 18. *Ancyloceras* (*Adouliceras*) gr. ex *mozambiquense-cooperi*. SAM–PCM5449, lateral view of shaft from Lubemba, Mozambique, Lower Aptian. Most common form, Form 1. × 0,77. B. *Ancyloceras* (*Ancyloceras?*) sp. indet. SAS B11 from locality 170, Zululand, Aptian I. × 1,55.

Fig. 19. *Ancyloceras* (*Adouliceras*) gr. ex *mozambiquense-cooperi*. SAM–PCM5337 from Lubemba, Mozambique, Lower Aptian. Most complete shaft of common form, Form 1. × 0,68.

Fig. 20. A–B. *Ancyloceras* (*Adouliceras*) gr. ex *mozambiquense-cooperi*. BMNH C78884 from locality 170, Zululand, Aptian I–II. Specimen with finer ribbing than previous examples. × 0,67.

Form 4

Fig. 21A

Description and discussion

Crozier SAS 54/45/6 completely lacks major ribbing on the ascending shaft. This crozier may be compared with *A.* (*Ad.*) *ewaldi* Dames (1880: 690, pl. 25, pl. 26 (fig. 1)). The latter species, however, has stronger and more rounded ribbing on the shaft. This specimen is crushed, hence no measurements are given.

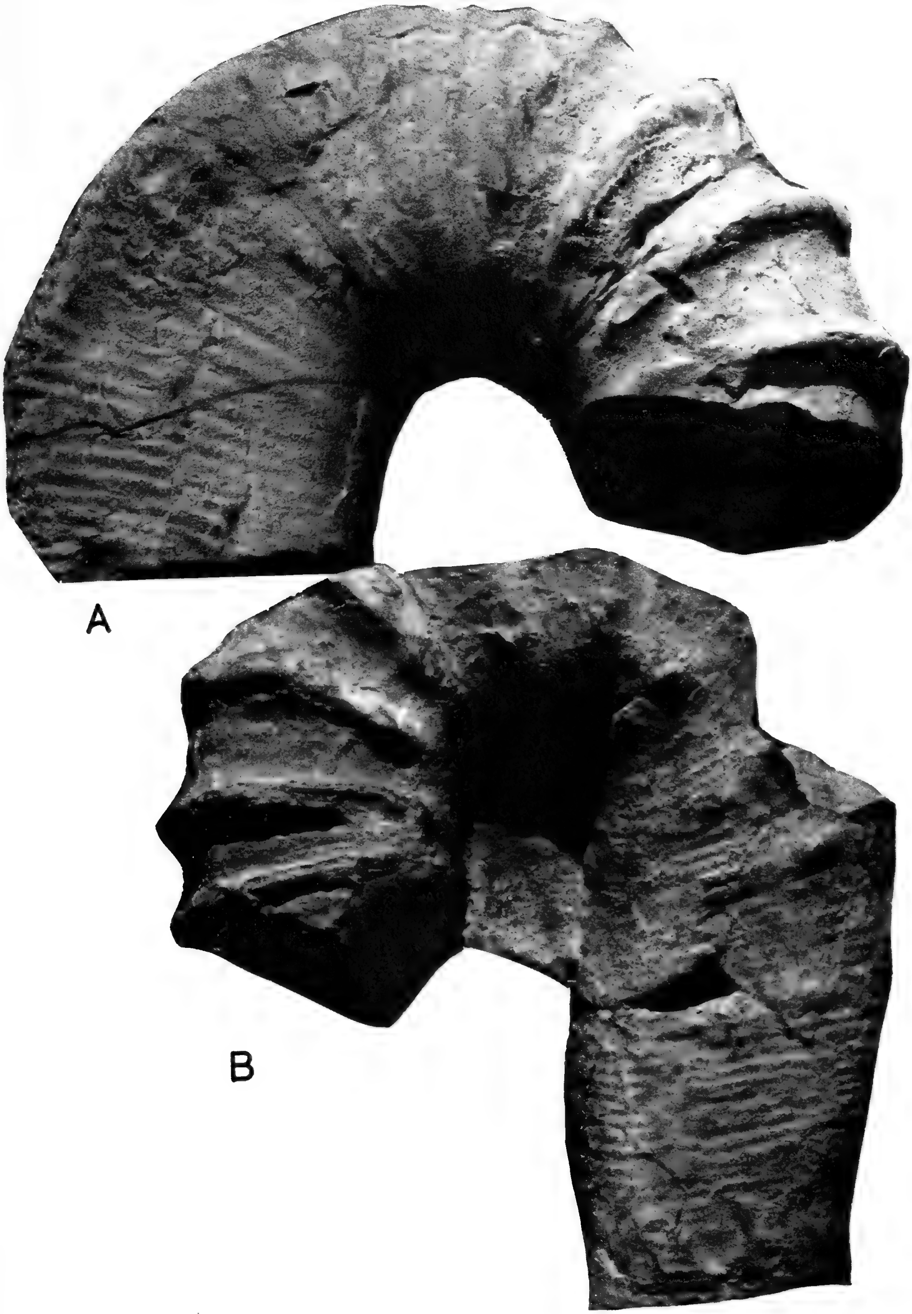


Fig. 21. A–B. *Ancyloceras* (*Adouliceras*) gr. ex *mozambiquense-cooperi*. A. SAS 54/45/6 from locality 170, Zululand, Aptian I–II. Form 4. × 0,57. B. SAS 54/45/5 from same locality and horizon as above. Form 2. × 0,53.

Form 5

Fig. 22

Description and discussion

Crozier SAS 54/45/4 is a micromorph with an ovoid whorl section on the shaft and with plain, simple ribbing throughout, apart from a smooth zone on the descending shaft and a slightly flared rib just before the aperture. A few paired ribs are more prominent than the others.

The rounded whorl section may indicate that this type of crozier may belong to the inner whorls referred to *A.* (*Ad.*) *cooperi* sp. nov. The absence of major costae on the crozier is reminiscent of that of *Colchidites colchicus* Djanélidzé (1926, pl. 1 (fig. 1)). The smooth part of the descending limb (which may be a malformation) is reminiscent of Anderson's (1938) genus *Shastoceras*. The body chamber of *Shastoceras*, however, is inflated and internal moulds are reportedly smooth.

Dimensions

Wb. at proximal end of shaft . .	54
Wh. at proximal end of shaft . .	57
Wb. in crozier	77
Wh. in crozier	*c.* 66
Wb. at aperture	80
Wh. at aperture	73
Width of crozier	175
Length of shaft to bend in crozier .	170

Form 6

Figs 9A, 24

Description and discussion

A single specimen, SAM–PCM5328 represents that part of a specimen at the point where the shaft begins curving into a crozier. Three sets of major ribs are present, separated by two to three low, rounded ribs. On the first major rib three rows of tubercles are present, of which the lateral one is best developed. At the distal end, however, only umbilical and lateral tubercles remain, but the lateral tubercle is enormous.

Viewed laterally there is resemblance to Murphy's *Ancyloceras thomeli* (1975: 24, pl. 3 (figs 1, 5), pl. 11 (figs 1–2)). In the Californian species, however, the ventral row of tubercles only appears towards the bend in the crozier, whereas the reverse holds true for the Zululand specimen.

Genus *Lithancylus* Casey, 1960

Type species

Hamites grandis J. de C. Sowerby, 1828 from the Lower Aptian of southern England by original designation of Casey (1960: 16).

Diagnosis

Coiling probably ancyloceratid, with a long, curved or straight shaft, ending in a recurved hook. Section of shaft circular to oval, sub-octagonal on crozier. Ornament consists of low, rounded oblique ribs on the shaft; towards the crozier trituberculate ribs occur.

Fig. 22. *Ancyloceras* (*Adouliceras*) gr. ex *mozambiquense-cooperi*. SAS 54/45/4 from locality 170, Zululand, Aptian I–II. Form 5. × 0,59.

Fig. 23. *Ancyloceras* (*Adouliceras*) gr. ex *mozambiquense-cooperi*. SAS 54/45/3 from locality 170, Zululand, Aptian I–II. Form 3. × 0,79.

Fig. 24. *Ancyloceras* (*Adouliceras*) gr. ex *mozambiquense-cooperi*. SAM–PCM5328 from Lubemba, Mozambique, Lower Aptian. Form 6. × 0,8.

Discussion

This is a relatively rare genus, characterized by the long, plainly ribbed shaft ending in a crozier with trituberculate ribs. The presence of an initial planispirally coiled part has yet to be demonstrated.

Apart from the type species, the genus is represented by *L. fustis* Casey (1961: 75, pl. 21 (fig. 4a–d)) from the Lower Aptian of southern England, *L. tirolensis* Casey (1961 : 74, text-fig. 29) from the Upper Barremian of Puez Alp, Tyrol, *L. mirabilis* Anderson (1938: 220, pl. 78 (figs 1, 2a, 3)), *L. nauplius* Anderson (1938: 221, pl. 66 (fig. 2–2a)), *L. neleus* Anderson (1938: 221, pl. 59 (fig. 2–2a)), and *L. cyclopius* Anderson (1938: 221, pl. 58 (fig. 3), pl. 66 (fig. 3–3a)), all from the Horsetown Beds of California, and probably of Barremian to Aptian age. *L. australe* Day (1967: 19, pl. 2 (figs 1–5), text-fig. 2) is from the Aptian of the Eromanga Basin of Queensland, Australia, and *L. guanacoensis*

Leanza (1970: 204, fig. III, 1–4) is reported from Patagonia. Thomson (1974: 15, pl. 2 (fig. 1) tentatively referred a specimen from Alexander Island (Falkland Island Dependencies) to *Lithancylus*. Reference of the Bulgarian specimen of *Ancyloceras elephas* Anderson, 1938 to *Lithancylus* by Dimitrova (1967: 61, pl. 29 (fig. 1)) is questionable. The Bulgarian specimen shows an inflated body chamber which is a characteristic of *Ancyloceras* (*Adouliceras*) rather than *Lithancylus*.

Differentiation of species is based mainly on the whorl section of the shaft and the density of ribbing thereupon.

Occurrence

Upper Barremian and Lower Aptian of England, Tyrol, California, Falkland Island Dependencies?, Patagonia, Mozambique and Australia.

Lithancylus sp.

Figs 25A–B, 83A, 84A–C

Material

SAM–PCM5436 from Lubemba, southern Mozambique.

Description

A straight, septate piece of shaft is probably referable to this genus. At the proximal end the whorl section is subtrigonal, with a broadly rounded dorsum and little-inflated flanks converging to a narrower, rounded venter. At the distal end the whorl section is virtually equidimensional, and octagonal. Ornament at the proximal end consists of low, rounded prorsiradiate ribs, separated by interspaces wider than themselves. It appears as if the ribs are weaker on the dorsum than on the flanks. At the distal end, three stronger trituberculate ribs occur, separated by two intermediary ribs. One pair of tubercles is situated ventrally, the other on the ventral third of the flanks and the third, which is smallest and virtually imperceptible, on the dorsal third of the flanks.

The suture line is very incised with trifid L, U and I lobes and bifid saddles.

Dimensions

Wb.	47,2	(at distal end)
Wh.	52,9.	

Discussion

This specimen corresponds approximately to Casey's *Lithancylus grandis* (Sowerby) specimen figured in his plate 20, fig. 1b, where ornament on the shaft changes from normal to trituberculate ribbing. *L. grandis*, however, has an almost circular whorl section on the shaft and is not conspecific. *L. fustis* has a depressed whorl section; *L. neleus* (Anderson), *L. mirabilis* (Anderson) and *L. australe* Day have ovoid whorl sections. *L. cyclopius* (Anderson) has a subtrigonal section as the present specimen, but finer ribbing, as has *L. tirolensis* Casey.

Thomson's (1974) *Lithancylus* sp. is poorly preserved, but appears to have finer ribbing at the proximal end.

Associated shafts of *Ancyloceras* (*Adouliceras*) spp. are all more massive and have finer ribbing.

Occurrence

Lower Aptian of southern Mozambique.

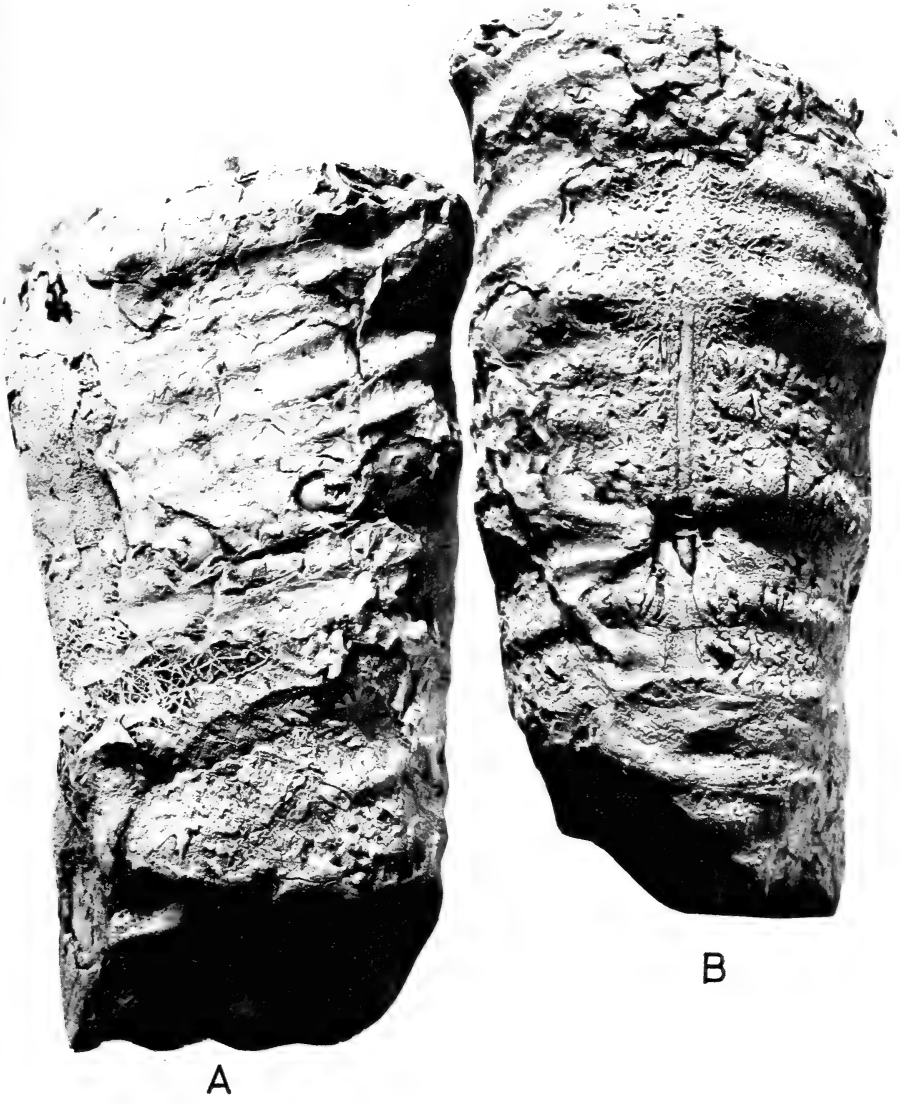


Fig. 25. *Lithancylus* sp. SAM–PCM5436 from Lubemba, Mozambique, Lower Aptian. × 1,2.

Genus *Tropaeum* J. de C. Sowerby, 1837

Type species

Tropaeum bowerbanki J. de C. Sowerby, 1837 from the Lower Aptian of England, by monotypy.

Diagnosis

Generally large; coiling predominantly crioceratitid, but in early species the body chamber may be distinctly uncoiled, giving rise to ancyloceratid or to aspinoceratid forms. Ornament on phragmocone consists of plain ribbing with occasional umbilical or ventral tubercles in early or late stages. On the body chamber a rapid change in ornament may take place, with the development of heavy, distantly spaced ribs. Aperture may be contracted. Dorsum ornamented by forward directed striae only.

Discussion

For details on the somewhat unusual manner in which the genus was introduced, and the accompanying nomenclatorial implications, see Casey (1960: 24), who also provides the most complete discussion of the genus. Additional information is provided by Day (1974: 5) who emended the diagnosis to accommodate loosely coiled forms and those in which no abrupt change in ornament takes place on the body chamber.

The best documented occurrences of *Tropaeum* are in England, the Caucasus and transcaspian regions of the U.S.S.R., and Australia. Recent descriptions of the English and Australian faunas are available, but for descriptions of the Russian species we are still heavily dependent on the older works of Sinzow (1872, 1905).

Together with the puzosiids, e.g. *P. seppenradensis* (Landois) and baculitids, e.g. *Baculites rex* Anderson and *Eubaculites latecarinatus* Brunnschweiler (unpublished data on Zululand specimens), *Tropaeum* are amongst the largest Cretaceous ammonites. Förster 1975*a*: 153) recently described a specimen of *Tropaeum subsimbirskense compressum* (Sinzow) from the Aptian of Mozambique with a diameter of over 900 mm. *Tropaeum imperator* Howchin & Whitehouse (1928: 487, figs 144–145) is reported to be over 770 mm in diameter (Casey 1960: 41). A body chamber fragment from Zululand to be described below measures *c.* 730 mm, and a virtually complete specimen 700 mm. The large size, and loose crioceratitid or even ancyloceratitid coiling of the genus suggests that *Tropaeum* may have been a poor swimmer and led a rather sluggish life.

With the exception of some species which may possess tubercles in the early or late stages, e.g. *Tropaeum imperator* Howchin & Whitehouse, the genus is easily distinguished from the other ancyloceratids by the general lack of tubercles.

Within the genus, three species groups, based on the coiling of the body chamber, may be recognized:

(i) *Tropaeum* gr. ex. *hillsi* J. de C. Sowerby
(ii) *Tropaeum* gr. ex. *bowerbanki* J. de C. Sowerby
(iii) *Tropaeum* gr. ex. *subarcticum* Casey

In each of these groups, successive species show parallel evolution of the outer whorls and body chamber with ancyloceratid, aspinoceratid and crioceratitid coiling respectively. This is a parallel development to that encountered in *Australiceras*, to be discussed below, and, as demonstrated by Casey (1960: 20, text-fig. 5), is one of the several examples of recoiling seen in ancyloceratids.

Specific differentiation amongst *Tropaeum* species is rather unsatisfactory, but is based primarily on the coiling of the outer whorls and body chamber, whorl section and ornamentation of the adult body chamber. Specific identification of fragments is usually virtually impossible. Species to be referred and possibly belonging to *Tropaeum* are as follows:

1. *Tropaeum? aegoceras* (von Koenen) (1902: 328, pl. 36 (fig. 1a–c)).
2. *Tropaeum arcticum* (Stolley) (1912: 16, pl. 2 (fig. 1)).
3. *Tropaeum australe* (Moore) (1870: 257, pl. 15 (fig. 3)).
4. *Tropaeum benstedti* Casey (1960: 37, pl. 3 (fig. 3), text-fig. 11g).
5. *Tropaeum bowerbanki* J. de C. Sowerby (1837: 535).
6. *Tropaeum bowerbanki* Sow. var. *densistriatum* Casey (1960: 30, pl. 6 (fig. 1)).
7. *Tropaeum caseyi* Collignon (1962: 18, pl. 222 (fig. 965)).
8. *Tropaeum drewi* Casey (1960: 35, pl. 8 (figs 1–2)).
9. *Tropaeum hillsi* (J. de C. Sowerby) (1836: 128).
10. *Tropaeum imperator* Howchin & Whitehouse (1928: 487, figs 144–145).
11. *Tropaeum keepingi* Casey (1960: 41, text-figs 11e, 13).
12. *Tropaeum? lamprum* (Etheridge Jun.) (1909: 157, pl. 48 (figs 1–2)). (According to Day (1974: 12) the holotype of this species is distinctly trituberculate and thus an *Australiceras*.)
13. *Tropaeum leptum* (Etheridge Jun.) (1909: 143, pl. 30 (figs 1–3), pl. 34 (fig. 2)).
14. *Tropaeum? multicingulatum* (Von Koenen) (1902: 314, pl. 34 (fig. 2)).
15. *Tropaeum rossicum* Casey (1960: 25).
16. *Tropaeum simbirskense* (Sinzow) (1872: 33, pl. 5 (figs 2–5), pl. 6 (figs 1–4)).
17. *Tropaeum subarcticum* Casey (1960: 40, pl. 8 (fig. 3a–c), pl. 10 (fig. 1), text-figs 11d, 12).
18. *Tropaeum subsimbirskense subsimbirskense* (Sinzow) (1905: 320, pl. 22 (figs 3–5)).
19. *Tropaeum subsimbirskense compressum* (Sinzow) (1905: 230, pl. 22 (figs 1–2)).
20. *Tropaeum undatum* Whitehouse (1926: 215).

Occurrence

Tropaeum occurs in the Aptian of England, northern Germany, the caucasian and transcaspian regions of the U.S.S.R., Bulgaria, Spitzbergen, eastern Greenland, arctic Canada, California, Japan, Patagonia, Falkland Island Dependencies?, Australia, Madagascar, Mozambique and Zululand.

Tropaeum sp. aff. *subsimbirskense subsimbirskense* (Sinzow, 1905)

Figs 26, 27A–B

Compare:

Crioceras subsimeirskense (*sic*) var. *inflata* Sinzow, 1905: 320, 330, pl. 22 (figs 3–5).

? Tropaeum subsimbirskense compressa: Dimitrova, 1967: 63, pl. 12 (fig. 1).

Material

SAS EM 109 from Manyola Drift, northern Zululand (26°50′20″S 32°13′5″E).

Description

Coiling is very involute, with an umbilical diameter of 33,5 per cent. The whorl section is rounded subtriangular with a flat dorsum, sharp umbilical edge and very little-inflated flanks converging to a sharp, narrow venter. The body chamber remains in contact with the phragmocone.

Ornament on the phragmocone consists of fine, sinusoidal ribbing. The ribs are faint on the dorsum and curve broadly forward. At the umbilical edge they curve sharply backward, forming a slight elevation, and then cross the flanks in sinusoidal fashion. Bifurcations and intercalations occur quite frequently at midflank or ventral thereof. On the nucleus, there are approximately seventy ribs per whorl. Towards the body chamber ornament gradually becomes coarser. On the earliest part of the body chamber virtually every rib bifurcates on the ventral quarter of the flanks, thus forming loops over the venter. Thereafter intercalated ribs arising on the ventral half of the body chamber replace the bifurcating ribs. On the last part of the body chamber, only strong, relatively high-crested ribs are present, separated by much wider interspaces. Each of these ribs has a prominent forward curvature over the venter. The suture line is very incised, with a huge lateral lobe.

Dimensions

Specimen	*D*	*Wb*	*Wh*	*Wb/Wh*	*U*
SAS EM 109	305	95(31,6)	112(37,2)	0,85	102(33,5)

Discussion

Casey (1960: 39 footnote) remarked that one of Sinzow's varietal names, *inflata* or *compressa* was superfluous, and subsequently regarded the variety *inflata* as representing *T. subsimbirskense* s.s. with Sinzow's (1905, pl. 22 (figs 4–5)) specimen as lectotype.

It should be pointed out here that the original spelling in the Russian text (Sinzow 1905: 320) is *subsimeirskense*, and *subsimbirskense* in the German résumé. The species is named after the Russian district of Simbirsk, and the name in the Russian text is obviously a typographical error. The valid name is thus *subsimbirskense*.

T. subsimbirskense subsimbirskense differs from the subspecies *compressum* in having a more inflated and depressed whorl section and a smaller umbilical diameter. Ribbing on the nominal subspecies also appears to be more sinusoidal when compared to the rursiradiate to rectiradiate ribbing of the subspecies *compressum*.

Dimitrova's (1967: 63, pl. 12 (fig. 1)) specimen is more suitably placed in the nominal subspecies rather than in *T. subsimbirskense compressum*.

Fig. 26. *Tropaeum* aff. *subsimbirskense subsimbirskense* (Sinzow, 1905). SAS EM 109 from Manyola Drift, Zululand, Aptian III. × 0,3.

Fig. 27. A–B. *Tropaeum* aff. *subsimbirskense subsimbirskense* (Sinzow, 1905). SAS EM109 from Manyola Drift, Zululand, Aptian III. × 0,34 and 0,55 respectively.

The Zululand specimen differs from *T. subsimbirskense subsimbirskense* mainly in not being quite as inflated and in lacking the strong major costae with intermediaries on the body chamber, and is hence referred to the Russian species in open nomenclature. The umbilical diameter of the Zululand specimen is intermediate between that of Sinzow's two figured specimens.

In the lack of a sudden change of ornament on the body chamber, the present species is similar to the Australian *Tropaeum undatum* Whitehouse 1926 (see Day 1974: 6, pl. 3 (fig. 2a–b)). The latter species has, however, a subquadrate whorl section and much stronger ribbing.

Occurrence

Aptian III of Zululand.

Tropaeum subsimbirskense compressum (Sinzow, 1905)

Figs 28, 29A–B, 37

Crioceras subsimeirskense var. *compressa* Sinzow, 1905: 320, pl. 22 (figs 1–2) (error).
Tropaeum mozambiquense: Da Silva, 1962: 24, pl. 9 (figs 1–2), pl. 12, *non* pl. 10, pl. 11, pls 13–14.
? Australiceras cf. *gigas:* Wachendorf 1967: 283 pl. 34 (fig. 4).
? Ammonitoceras tovilense: Wachendorf, 1967: 282, pl. 36 (fig. 1).
Tropaeum subsimbirskense compressum: Förster, 1975*a*: 152, pl. 2 (figs 3–6), text-fig. 29. *Non* Dimitrova, 1967: 63, pl. 12 (fig. 1).

Lectotype

Sinzow's (1905, pl. 22 (fig. 1)) specimen is herein designated lectotype. So far as can be determined, Sinzow did not designate a holotype. Dimitrova (1967: 63) stated that Sinzow's plate 22, figure 1 specimen is the type, but this cannot be taken as a lectotype designation.

Material

SAS EM 110 from Manyola Drift, Zululand. Aptian III.

Description

Coiling is closely crioceratitid with no sign of uncoiling of the body chamber. The innermost whorls, up to a diameter of 75 mm, are not preserved. At a diameter of 160 mm the whorl section is subtriangular with a flat to concave dorsum, a sharp umbilical edge, very little-inflated flanks and a narrow venter. Apart from the fact that the whorl height increases more rapidly than the whorl breadth, the whorl section remains basically subtriangular up to the body chamber. On the body chamber the umbilical wall becomes more rounded, the umbilical edge less acute and the flanks more inflated. The whorl section becomes subrectangular at this stage.

On the inner whorls, ornament consists of single, low, rounded rursiradiate to radial ribs separated by interspaces of the same width. At a diameter of approximately 300 mm occasional stronger ribs occur, separated by three to five

Fig. 28. *Tropaeum subsimbirskense compressum* (Sinzow, 1905). SAS EM110 from Manyola Drift, Zululand, Aptian III. × 0,25.

normal ribs which may bi- or trifurcate at the umbilical edge. Towards the end of the phragmocone the major ribs become stronger. The beginning of the body chamber is marked by a very strong, low broad rib. From here onward, as far as the aperture, ornament consists solely of ten widely spaced, initially low, broad ribs; the intercalatories having disappeared completely. Towards the aperture, the last four or five major ribs become progressively flared and narrower on the flanks, and also closer spaced. The first three to four major ribs on the body chamber are restricted to the flanks, but towards the aperture, as they become increasingly flared, they bifurcate at the ventral edge and cross the venter as

Fig. 29. A–B. *Tropaeum subsimbirskense compressum* (Sinzow, 1905): SAS EM110 from Manyola Drift, Zululand, Aptian III. × 0,34.

very low, broad looped folds. The last three or four ribs before the aperture are the most prominent, being thin and flared on the flanks and broad and high over the venter.

Part of the aperture is preserved. It appears to have been simple, and somewhat constricted.

The suture is very incised and dentritic, consisting of a trifid L, U and I. The lateral lobe is largest and occupies virtually the whole of the flank (see Fig. 87).

Dimensions

Specimen	*D*	*Wb*	*Wh*	*Wb/Wh*	*U*
SAS EM110	510	140(27)	151(29)	0,93	222(43)
	390	109(27)	139(35)	0,80	163(44)

Discussion

The main characteristic features of the phragmocone of this species are the whorl section, with little-inflated flanks, converging to a narrow dorsum (see Förster 1975*a*, text-fig. 29), and the more or less straight, rursiradiate ribbing. On the body chamber, the low, major costae, separated by wide interspaces and devoid of intercalatories are equally characteristic.

The lectotype (Sinzow 1905, pl. 22 (fig. 1)) specimen does not have quite as prominent major costae as the Zululand or Mozambique material, but it appears that only a part of the body chamber is preserved. The last part of the outer whorl on the lectotype also is slightly detached. Illustrations of *T. bowerbanki* in Casey 1960 (compare pl. 4 (fig. 1) and pl. 5 (fig. 1)), however, show that there is some degree of variation in the tightness of coiling of the outer whorl in *Tropaeum*, and that it can be included in the range of intraspecific variation.

The closest European ally to this species is *Tropaeum bowerbanki* J. de C. Sowerby, from which the present form appears to have been derived. The major differences are that the flanks are more convergent on the phragmocone in *T. subsimbirskense compressum* than in *T. bowerbanki*, whilst the body chamber of *T. bowerbanki* is also more robust; the ribs are flared and high-crested, compared to the low, broad ribs in *T. subsimbirskense compressum*.

As yet no Malagasy equivalent of this species has been described.

Förster (1975*a*) has shown that specimens occur with a diameter in excess of 900 mm, surpassing all other records of large *Tropaeum*.

Occurrence

Upper Aptian of Mangyschlak, southern Russia, Bulgaria ?, Mozambique and Zululand.

Tropaeum rossicum Casey, 1960

Figs 30, 31B

Ancyloceras gracilis, Sinzow, 1872: 35, pl. 6 (figs 5–6, 10–11).
Crioceras gracile Sinzow, 1905: 306, pl. 17 (figs 1–4), pl. 18 (fig 6), pl. 19 (fig. 1).
Tropaeum rossicum Casey, 1960: 43.

Material

SAM–PCZ5681 from an unknown locality in Zululand.

Holotype

Sinzow's (1905, pl. 18 (fig. 1)) specimen from Stepnaja, Simbirsk.

Description

The available specimen consists of just over one whorl. Coiling is loose, with the whorls just touching but not impressed. The whorl section is ovoid,

Fig. 30. *Tropaeum rossicum* Casey, 1960. SAM–PCZ5681 from an unknown locality in Zululand. × 0,57.

Fig. 31. A. *Australiceras wandalina* (Boshoff MS) sp. nov. SAS EM106 from Manyola Drift, Zululand, Aptian III. × 0,69. B. *Tropaeum rossicum* Casey, 1960. SAM–PCZ5681 from an unknown locality in Zululand. × 0,6.

higher than wide on the early part of the whorl, but becomes more rounded on the outer part. Ornament consists of approximately 100 strong, rursiradiate, rounded ribs, separated by interspaces of equal width. Initially, ribbing is quite prominent on the umbilical wall, but eventually becomes quite faint at the largest diameter preserved. The ribs cross the flanks and venter without interruption.

Discussion

Casey (1960: 43) drew attention to the fact that *Ancyloceras gracile* Sinzow, 1872 was a homonym of *Ancyloceras gracile* Oppel *in* Zittel 1868 and that a new name was required. Being uncertain as to whether Sinzow's 1872 (pl. 6 (figs 5–6, 10–11)) immature specimens of *Ancyloceras gracile* were conspecific with his (Sinzow's) 1905 specimens of *Crioceras gracile*, Casey designated Sinzow's (1905 pl. 18 (fig. 1)) specimen as holotype of *Tropaeum rossicum*.

With only one specimen available, it is impossible to comment on the relationship of Sinzow's 1872 and 1905 specimens, and the species is here interpreted on the basis of the 1905 specimens. Sinzow (1905, pl. 19 (fig. 1)) illustrated a specimen with finer ribbing with which the Zululand specimen compares well. The whorl section provided by Sinzow (1905: 308) also corresponds to that of the present specimen. No sign of ventral tuberculation is present, but according to Sinzow this only is present in the early and late stages.

T. rossicum is easily distinguished by the ovoid whorl section on the phragmocone, the strong, rounded and relatively straight, rursiradiate ribbing. *T.* sp. aff. *undatum* Whitehouse, to be described below, has similar ornament on the inner whorls, but shows a rapid increase of whorls and a square whorl section. *T. drewi* Casey (1960: 35, pl. 8 (figs 1–2), pl. 9 (fig. 1), text-figs 10, 11f) has a similar rib density (*c.* 90 at 150 mm diameter), but ribbing is more or less radial and the whorl section compressed.

Tropaeum caseyi Collignon (1962: 18, pl. 222 (fig. 965)) has a similar, but much coarser style of ribbing.

By the possession of tuberculation in the early and late stages, *T. rossicum* occupies an intermediate position between *Tropaeum* and *Australiceras*. Casey (1960: 25) refers to *T. rossicum* as being intermediate between *T. hillsi* and *A. gigas*, both forms with a body chamber terminating in a straight shaft and hook. It is not quite clear if this is meant to imply a hook-shaped body chamber in *T. rossicum*. Sinzow's figures and his comparisons with *T. bowerbanki* indicate, rather, that the coiling was aspinoceratid or crioceratitid.

Occurrence

T. rossicum is only known from the Aptian of Simbirsk and Zululand. Casey recorded *Tropaeum* cf. *rossicum* from the Upper Aptian *martini* Zone of Maidstone, Kent.

Tropaeum dayi sp. nov.

Figs 32–34

Tropaeum cf. *australe:* Day, 1974: 5, pl. 1 (fig. 1a–b), pl. 2 (fig. 2a–b).

Holotype

SAS EM109b from Manyola Drift, northern Zululand, Aptian III. Collected by the late Mr E. Meyer.

Derivation of name

Named after Dr R. Day, Geological Survey of Queensland, Brisbane.

Description

The innermost whorls are not preserved. Coiling is open, crioceratitid, with the whorls not touching. The body chamber becomes a little detached. The whorl section is compressed with a rounded dorsum lacking a zone of impression, a broadly rounded umbilical edge, weakly inflated flanks and a broadly rounded venter. Ornament on the early whorls consists of delicate, thin ribs, separated by wider interspaces. The ribs are straight to sinuous on the flanks and cross the dorsum and venter with a forward curvature. Rib density is *c.* 100 at a diameter of 150 mm. With increasing diameter ribbing becomes coarser, but there is no abrupt change in ornament on the body chamber. On the body chamber of the holotype, of which half a whorl is preserved, twenty-six ribs occur per half whorl. Ribbing on the body chamber is broad and low, with very faint traces of tuberculation on the last few ribs. The aperture is unknown.

The suture is minutely frilled. The lateral lobe is largest, asymmetrical and occupies virtually the whole of the flanks (see Fig. 34).

Dimensions

Specimen	*D*	*Wb*	*Wh*	*Wb/Wh*	*U*
SAS EM 109b	285	110(28,5)	140(36,3)	0,78	157(40,7)

Discussion

Apart from slight differences in relative proportions, the Zululand specimen and the Australian specimen figured by Day (1974: 5, pl. 1 (fig. 1a–b), pl. 2 (fig. 2a–b)) as *Tropaeum* cf. *australe* are virtually identical. Ornament on the inner and outer whorls is the same and both lack a sudden change in ornament at the beginning of the body chamber. The loose coiling is conspicuous in both forms and serves to distinguish it from *T. australe* (Moore). *T. australe* (Moore) is a poorly-known species, but from the available illustrations (Moore 1870, pl. 15 (fig. 3); Etheridge Jun. 1892, pl. 31 (fig. 1), pl. 32 (figs 3–4)) it can be seen that ornamentation and whorl section are similar to those of the present species, but that the coiling is closer with the whorls touching.

Australiceras rabenjanaharyi Collignon (1962: 26, pl. 226 (fig. 969)) from Madagascar, has similar ornament after the initial trituberculate stage, but is also tightly coiled with the whorls touching.

Tropaeum rossicum Casey, 1960 has a similar whorl shape but ribbing is much coarser and ornament on the body chamber differs from that of *T. dayi* sp. nov.

The presence of faint tubercles on the inner whorl of this species (Day, 1974: 5) indicates that it is somewhat intermediate between *Tropaeum* and *Australiceras*, as is the case in *T. rossicum*.

Occurrence

The Australian specimens are from the Aptian of the Eromanga and Surat basins. The Zululand specimen is from the authors' Aptian III.

Fig. 32. *Tropaeum dayi* sp. nov. SAS EM109b, holotype from Manyola Drift, Zululand. Aptian III. × 0,32.

Fig. 33. A–B. *Tropaeum dayi* sp. nov. SAS EM109b, holotype from Manyola Drift, Zululand, Aptian III. × 0,42.

Fig. 34. *Tropaeum dayi* sp. nov. SAS EM109b. Suture line of holotype. × 1.

Tropaeum obesum sp. nov.

Figs 35–37, 38D, 39–42, 65E

Holotype

SAM–PCZ5681 from locality 34, Zululand. Aptian IV. Housed in the South African Museum. Collector unknown.

Material

The holotype and SAS A4000 from locality 34, Aptian IV, and numerous fragments from locality 168, Aptian IV, including BMNH C7885. BMNH C78886–C8887 are from the same horizon at locality 171.

Description

Very large, coiling is crioceratitid with the whorls touching and with a dorsal zone of impression. The body chamber remains in contact with the phragmocone. The whorl section is initially subtrigonal, slightly higher than wide with rounded umbilical edges, moderately inflated flanks and a narrow rounded venter. With increasing diameter the whorl section becomes more inflated and rounded. On the body chamber, which consists of about half a whorl in the holotype, the section becomes depressed.

Ornament is variable, but consists mostly of slightly sinusoidal ribs on the phragmocone. They are generally inclined backward, but may on occasion be radial. Over the dorsum the ribs are reduced to striae with a strong forward curvature. With increasing diameter ribbing becomes coarser, and the body

Fig. 35. *Tropaeum obesum* sp. nov. SAM–PCZ5681, holotype from locality 34, Zululand, Aptian IV. Area between X–X restored. × 0,22.

Fig. 36. *Tropaeum obesum* sp. nov. SAM–PCZ5681 holotype from locality 34, Zululand, Aptian IV. Restored part removed. × 0,26.

Fig. 37. *Tropaeum obesum* sp. nov. SAS A4000 from locality 34, Zululand, Aptian IV. Inner whorls up to X sculpted in matrix. × *c*. 0,5.

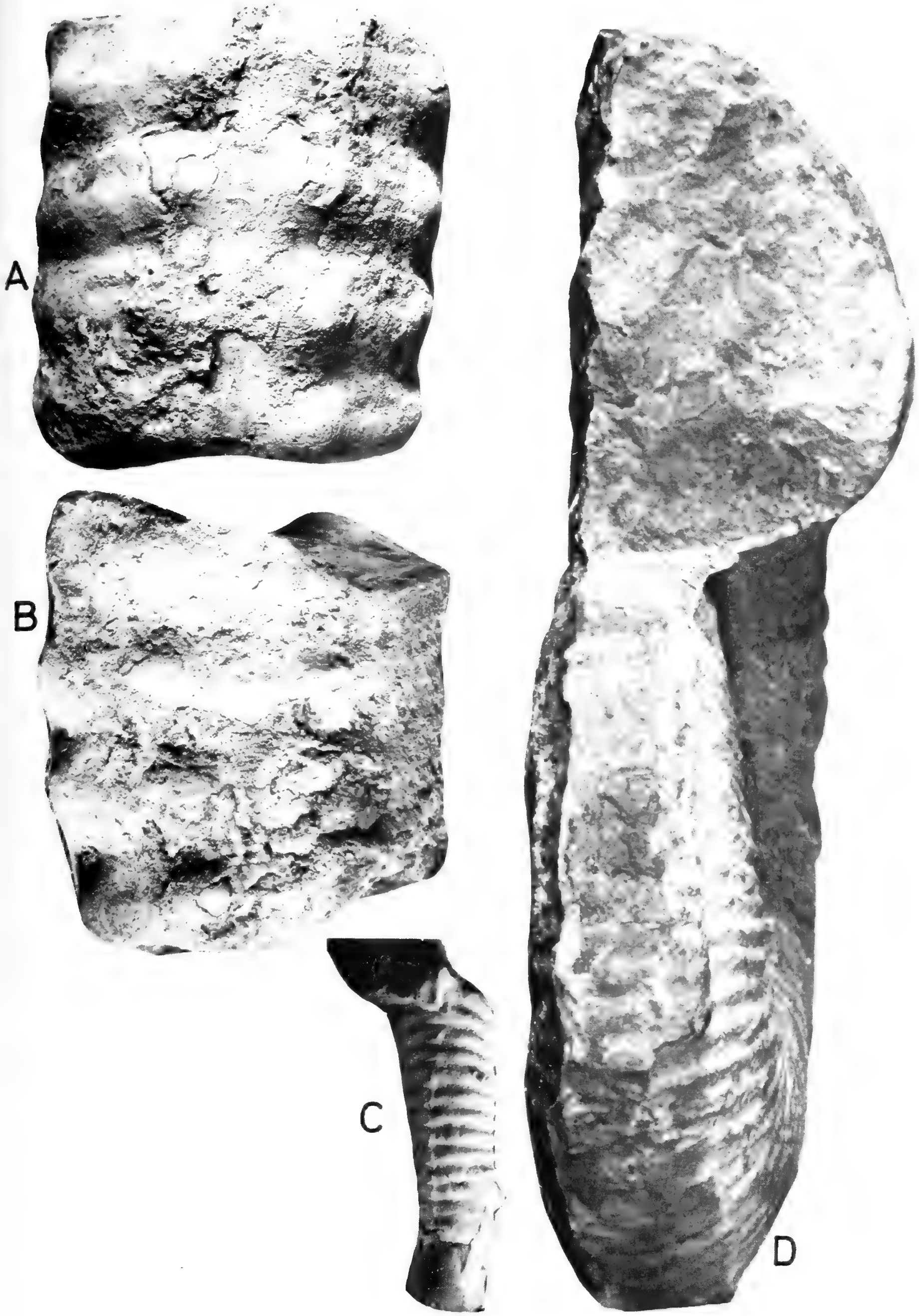


Fig. 38. A–B. *Australiceras* sp. indet. A. SAS L3 from locality 170, Zululand, Aptian I–II. × 1. C. *Tonohamites aequicingulatus* (von Koenen, 1902). SAS Z8/Ta1 from locality 168, Aptian III–IV. × 1,5. D. *Tropaeum obesum* sp. nov. SAS A4000 from locality 34, Zululand, Aptian IV. × *c*. 0,5.

Fig. 39. A–B. *Tropaeum obesum* sp. nov. BMNH C78886, fragment from locality 171, Zululand, Aptian IV. × 1.

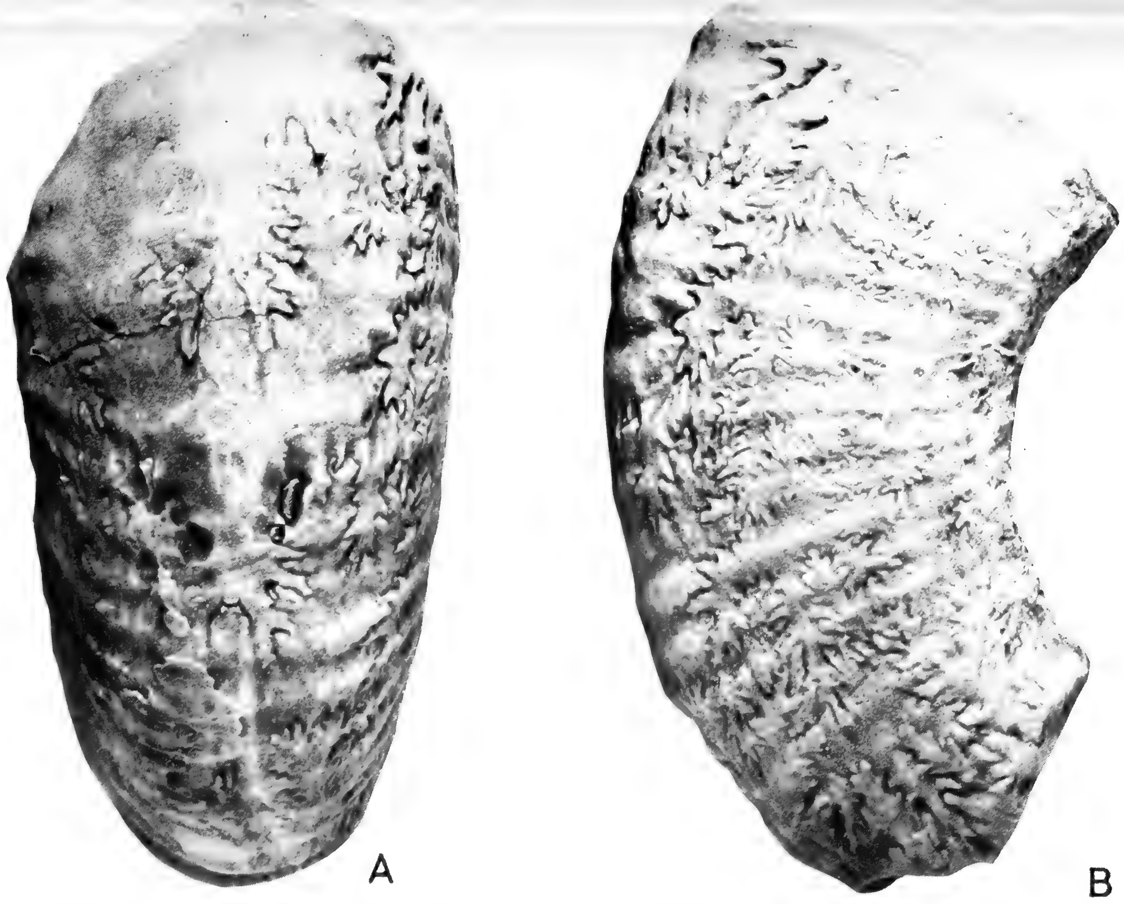


Fig. 40. A–B. *Tropaeum obesum* sp. nov. BMNH C78887, fragment from locality 171, Zululand, Aptian IV. × 0,7.

Fig. 41. *Tropaeum obesum* sp. nov. BMNH C78885 from locality 168, Zululand, Aptian IV. × 0,9.

Fig. 42. *Tropaeum obesum* sp. nov. BMNH C78885 from locality 168, Zululand, Aptian IV. × 0,9.

chamber bears about twelve heavy, laterally flared, sharp-crested ribs. Over the venter, these ribs are broad and low. Major ribs are also absent on the dorsum and only striae occur.

The suture line is characterized by thin-stemmed saddles and a large asymmetrically trifid lateral lobe.

Dimensions

Specimen	*D*	*Wb*	*Wh*	*Wb/Wh*	*U*
SAM–PCZ5681	630	250(39,9)	210(33,4)	1,18	260(41)

Discussion

Numerous fragments of *Tropaeum* are tentatively referred to this species which is characterized by its rounded adult whorl section and generally rursiradiate sinusoidal ribs.

Tropaeum imperator Howchin & Whitehouse (1928: 487, figs 144–145) is a similar large species with comparable ornament on the phragmocone. The whorl section on the final whorl, however, is subquadrate, compared to rounded depressed in the present species. Apparently, coiling in *T. imperator* is loosely crioceratitid, whereas that of *T. obesum* sp. nov. is tight, with the inner whorls touching.

Tropaeum percostatum (Gabb) (1864: 77, pl. 16 (fig. 26), pl. 17 (fig. 26a)); (see also Anderson, 1938: 212, pl. 71 (fig. 1), pl. 72 (fig. 1) is a related species with denser, lower ribbing on the body chamber. The whorl section of the latter species is subquadrate, compared to rounded-depressed in *T. obesum*. The body chamber of *T. percostatum* is said to become slightly detached.

Crioceras aegoceras von Koenen (1902: 328, pl. 36 (figs 1a–c, 2–3)) has similar ornament on the outer whorl, but coarser costation on the inner whorls than *T. obesum* sp. nov., and is only doubtfully referred to *Tropaeum*.

Occurrence

Upper Aptian of Zululand.

Tropaeum sp. aff. *undatum* Whitehouse, 1926

Figs 43–44

Compare:

Tropaeum undatum: Jeletzky, 1964: 68, pl. 20 (fig. 2). Hill, Playford & Woods, 1968: K16, pl. K7 (fig. 3). Day 1974: 6, pl. 3 (figs 2a–b).

Tropaeum rarum Whitehouse, 1926: 216, pl. 36 (fig. 1a–b).

Material

SAS UMS1 from locality 34, Mzinene River. Aptian IV.

Description

In the Zululand specimen parts of three whorls are still in contact. Coiling is crioceratitid with the whorls just touching. On the innermost whorl the section is square, but with increasing diameter soon becomes subtrigonal and higher than wide. The dorsum is flat, with a slight dorsal zone of impression on the last whorl, rather sharp umbilical edges and little inflated flanks converging to a broadly rounded venter.

On the innermost whorl still preserved, ornament consists of very strong, broad, slightly rursiradiate single ribs; approximately five in a distance equal to the whorl height. On the succeeding whorl ornament becomes finer, the ribs are weak over the dorsum, crossing it with a slight forward flexure, then passing backwards over the umbilical wall and flexing backwards over the flanks. A few bifurcations occur on the dorsal third of the flanks. Eight ribs occur in a distance equal to the whorl height on the second preserved whorl, and on the last whorl ribbing is very coarse and widely spaced, with five to six ribs per whorl height.

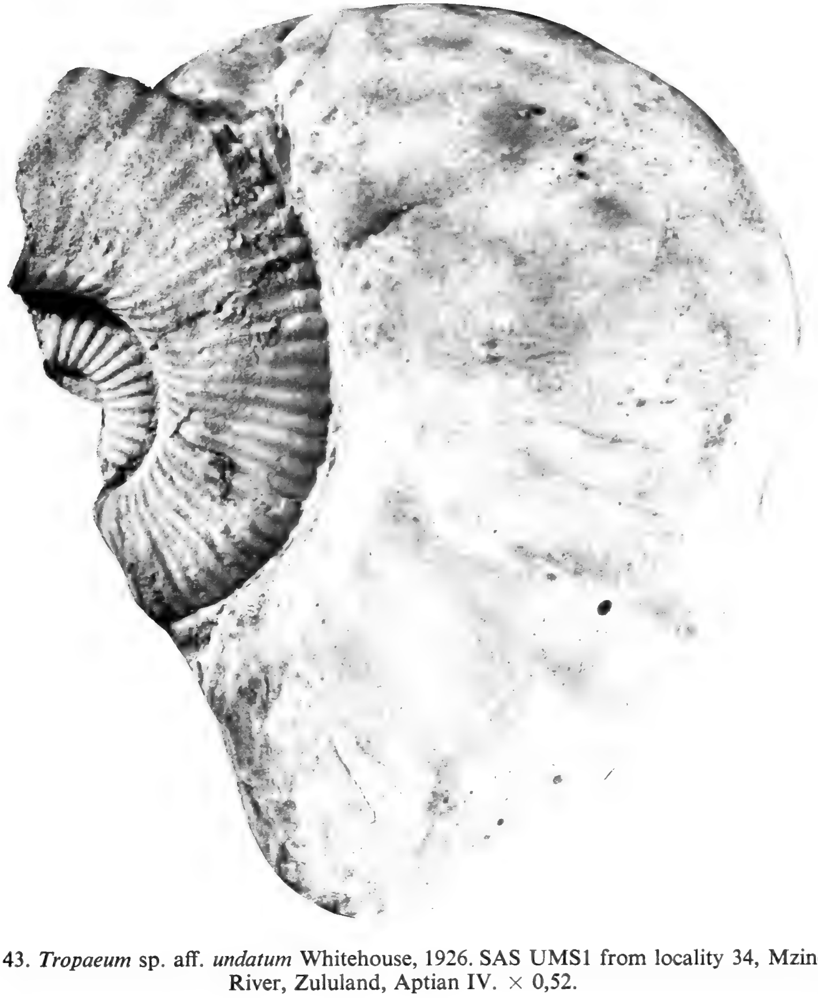


Fig. 43. *Tropaeum* sp. aff. *undatum* Whitehouse, 1926. SAS UMS1 from locality 34, Mzinene River, Zululand, Aptian IV. × 0,52.

Discussion

Tropaeum rarum Whitehouse, 1926 was included in the synonomy of *T. undatum* by Day (1974: 6, 7). The Zululand specimen is tentatively referred to the Australian species because of the similar coarse ribbing on the innermost whorls, followed by slightly sinuous ribbing, together with a rapid increase in whorl diameter. The only obvious difference is that the whorl section of the Australian material is square to depressed, compared to the compressed, higher than wide outer whorl of the Zululand specimen.

Crioceras australe Waagen, 1875 *non* Moore, is superficially similar as

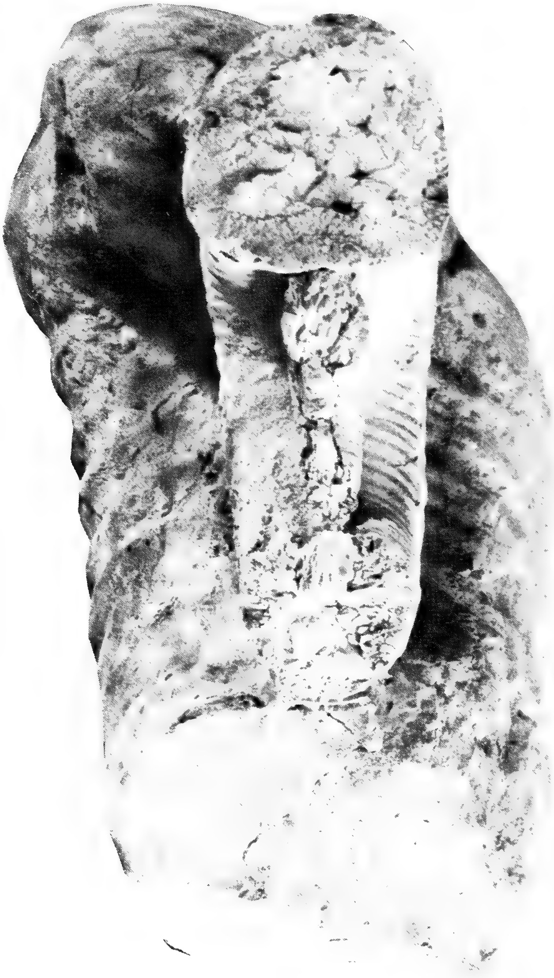


Fig. 44. *Tropaeum* sp. aff. *undatum* Whitehouse, 1926. SAS UMS1 from locality 34, Mzinene River, Zululand, Aptian IV. × 0,58.

regards the rapid increase in whorl diameter, but is, of course, generically distinct, belonging to *Australiceras*.

The rapid increase in whorl diameter and the coarse ribbing of inner and outer whorls, together with finer ribbing during middle growth stages, clearly distinguish this species from the other Zululand *Tropaeum*.

Occurrence

Upper Aptian, Aptian IV of Zululand.

Tropaeum sp. gr. ex *bowerbanki* (J. de C. Sowerby) var. *densistriatum* Casey—*T. hillsi* (J. de C. Sowerby)

Fig. 45

Compare:

Tropaeum bowerbanki (J. de C. Sowerby) var. *densistriatum* Casey, 1960: 30, pl. 6 (fig. 1).
Tropaeum hillsi: Casey, 1960: 30, pl. 7, text-figs 8–9, 11c.

Material

SAS L3 from locality 170 Mlambongwenya Creek, Zululand. Lower Aptian, Aptian I or II.

Description

One specimen consisting of parts of two embracing whorls is available. Coiling is open, crioceratitid, and the whorls are not in contact. The specimen is slightly crushed, but the whorl section appears to have been rounded-subrectangular, with a rounded venter narrower than the dorsum. The flanks and venter are ornamented by approximately fifty radial ribs per half whorl. The dorsum is smooth and devoid of ribbing.

Discussion

The specimen is from the horizon of abundant *Ancyloceras* (*Adouliceras*) spp. The absence of tuberculation on the inner whorl, however, clearly shows that it is a *Tropaeum*.

The whorl section and density of ribbing are the same as those of *Tropaeum bowerbanki* var. *densistriatum* (Casey 1960: 31, pl. 6 (fig. 1)) and *Tropaeum hillsi* (J. de C. Sowerby) (see Casey 1960: 31, pl. 7, text-figs 8–9, 11c). The inner whorls of these two species are indistinguishable (Casey 1960: 33). For the present it is therefore only possible to refer to this specimen as *Tropaeum* sp. gr. ex. *T. bowerbanki* var. *densistriatum*—*T. hillsi*. As Casey has shown (1960: 33) the two species are very close and connected by transitional forms. Because of differences in age, however, he maintained the two species apart.

Tropaeum subsimbirskense (Sinzow) (1905: 320, pl. 22 (figs 1–5)) has similar inner whorls, but the flanks are strongly convergent to the venter.

Occurrence

T. hillsi occurs in the Lower Aptian, top of the *deshayesi* Zone in England. *T. bowerbanki* var. *densistriatum* is ubiquitous in the *bowerbanki* Zone of Kent, England.

Fig. 45. *Tropaeum* sp. gr. ex *bowerbanki* var. *densistriatum-hillsi.* SAS L3 from locality 170, Zululand, Aptian I or II. × 1,1.

Tropaeum sp. indet.

Fig. 46

Material

SAS Z804 from locality 151, Mkuze Game Reserve, Aptian IV.

Description and discussion

A massive body chamber fragment, approximately 730 mm long, is of interest in that it is filled with abundant small tonohamitids (to be described below).

The whorl section is wider than high with a slight dorsal zone of impression. Ornament consists of about fifteen heavy, sharp ribs. Ribbing is restricted to the flanks and venter. The dorsum is ornamented by forwardly directed striae, not corresponding in number to the lateral ribs.

Although the inner whorls are not preserved the stratigraphic horizon is one that is characterized by *Tropaeum* with crioceratitid coiling, and the body chamber more or less in contact with the rest of the phragmocone.

The present specimen may be compared with *Tropaeum subarcticum* Casey (1960: 40, pl. 8 (fig. 3a–c), pl. 10 (fig. 1), text-figs 11d, 12) which also grows to great size. Ribbing on *T. subarcticum* is denser, however, and some of the ribs on the body chamber illustrated by Casey (1960: 40, text-fig. 12) are looped, bifurcating near the venter.

Tropaeum imperator Howchin & Whitehouse (1928: 487, figs 144–145), another gigantic species from the Aptian of Australia, has much sharper, and more distantly spaced ribbing on the body chamber. *Tropaeum obesum* sp. nov. has a more inflated whorl section and more distantly spaced ribs on the body chamber.

Genus *Australiceras* Whitehouse, 1926

(= *Colombiaticeras* Royo y Gomez, 1945)

Type species

Crioceras jacki Ethridge Jun., 1880 from the Aptian of eastern Australia by original designation Whitehouse (1926: 208).

Diagnosis

Coiling ancyloceratid or aspinoceratid in early Aptian species, but crioceratitid in later ones. Early whorls not always in one plane; ornamented by trituberculate ribs separated by a variable number of intermediaries. Tuberculation ceases at variable diameters in middle stages of growth and may or may not reappear on the body chamber.

Discussion

Whitehouse originally introduced *Australiceras* for crioceratitid forms only, a view followed by Wright (1957: L211). Latterly, the genus has been taken to

Fig. 46. *Tropaeum* sp. indet. SAS Z804 from locality 151, Zululand, Aptian IV. Large body chamber fragment with last septum preserved and filled with numerous specimens of *Tonohamites? caseyi* sp. nov. Photograph by courtesy of Tony Harris (Salisbury). × *c.* 0,24.

include the early Aptian representatives of the lineage with ancyloceratid coiling. The extent and variability of the early Aptian representatives of the genus in the English Lower Greensand was exhaustively reviewed by Casey (1960, 1961), as was the scope of the Australian late Aptian representatives by Day (1974). Unfortunately, however, little or no work has been done on the Central European or Soviet material since the beginning of the century.

Spath (1931: 656) advocated that the name *Australiceras* be abandoned in favour of *Tropaeum*, due to the difficulty encountered in deciding whether or not tuberculation was present, especially in fragmentary material. Transitional forms do occur, for example *Australiceras pingue* Casey, *T. rossicum* Casey, and *T. imperator* Howchin & Whitehouse, but both genera are accepted as valid taxa. For a further discussion on the differences between *Tropaeum* and *Australiceras*, see Casey (1960: 40, 1961: 45). Day's (1974: 8) assertion that the saddles of the suture lines of the Australian representatives of *Australiceras* tend to be broader than those in *Tropaeum* is also true to a certain extent in the Zululand material, and it appears that in some late Aptian species the saddles tend to become broader, accompanied by a general simplification of the suture line.

Differences between the homoeomorphic *Ancyloceras* (*Adouliceras*) and the early uncoiled forms of *Australiceras* are discussed elsewhere (p. 226).

As in *Tropaeum*, three species groups are recognized, based on the coiling.

(i) *Australiceras* gr. ex. *gigas* (J. de C. Sowerby)
(ii) *Australiceras* gr. ex. *tuberculatum* (Sinzow)
(iii) *Australiceras* gr. ex. *jacki* (Etheridge)

Specific differentiation is a moot point, as it is in *Tropaeum*. Virtually all the species described from the Eurasian, Australian, North American, South American and Madagascan regions appear to be endemic to these regions, and either based on unique type specimens, or, if based on large collections, are interpreted so widely that differences between the various species are difficult to formulate, all of which suggests a superfluity of specific names, and high intraspecific variability.

The diameter at which tuberculation ceases is variable, as has been illustrated in *A. gigas* (see Casey 1961: 47) and *A. jacki* (see Day 1974: 9). Rib density and whorl section in the early stages seem to be equally unreliable specific characters in *A. jacki* as shown by Day (1974: 9) and also here in Figures 47–49, based on Australian material housed in the British Museum (Natural History).

The only apparent differences of use in specific separation are the coiling of the body chamber, whorl section, and rib density in the adult stage together with, to a lesser degree, strength of tuberculation and the number of intermediaries in the early stages.

Species to be referred to *Australiceras* are as follows:

1. *Australiceras argus* Anderson (1938: 211, pl. 70 (figs 1–2)).
2. *Australiceras australe* (Waagen *non* Moore) (1875: 246, pl. 60 (fig. 1)).

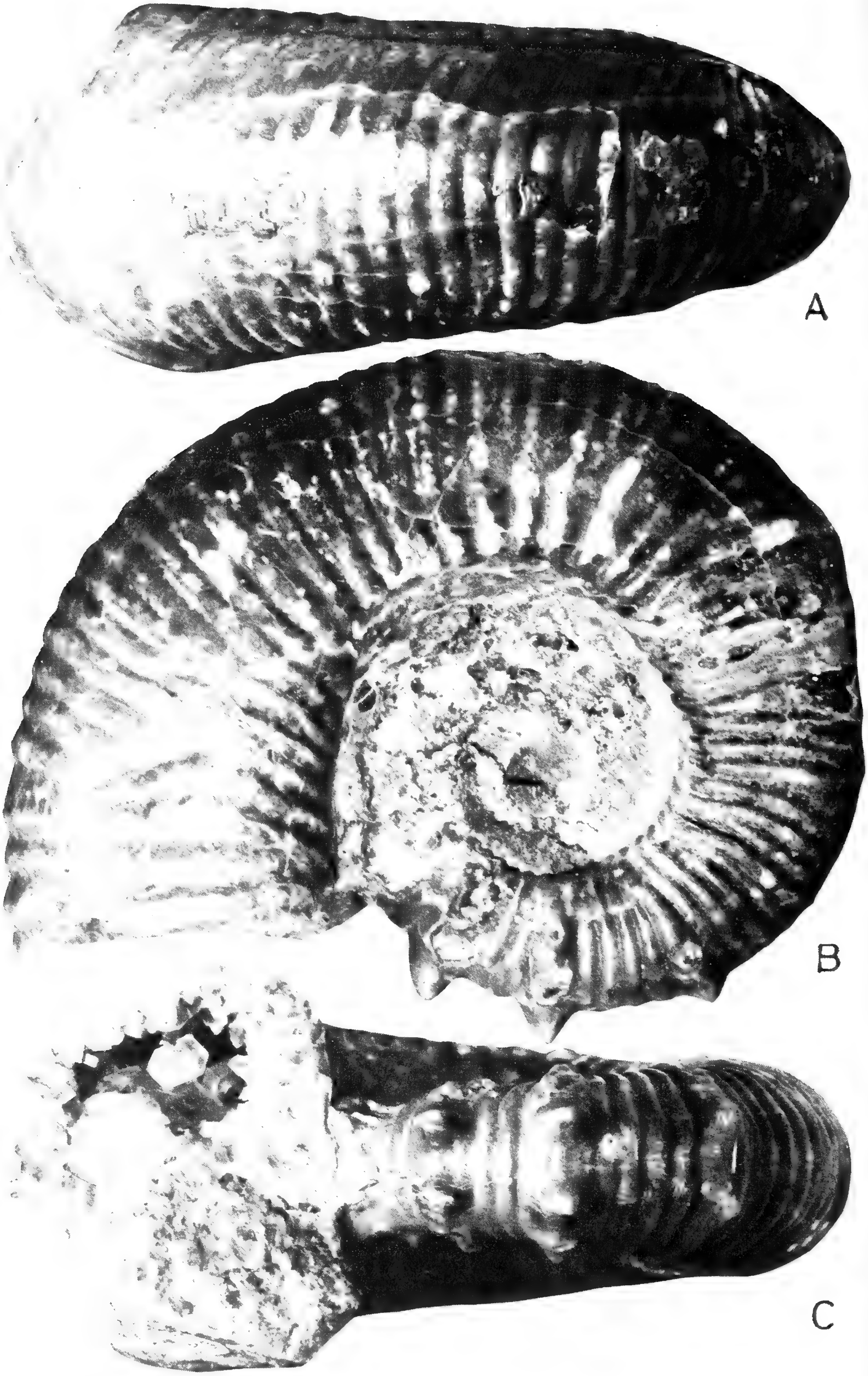


Fig. 47. *Australiceras jacki* (Etheridge Jun., 1880). BMNH C40769 from the Aptian of Rolling Downs, Queensland, Australia. × 1.

Fig. 48. *Australiceras jacki* (Etheridge Jun., 1880). BMNH C40760 from the Aptian of Rolling Downs, Queensland, Australia. Note the pathological body chamber. × 1.

3. *Australiceras bolivari* (Royo y Gomez) (1945: 470, pl. 75 (fig. 2)).
4. *Australiceras? bulgaricum* Dimitrova (1967: 62, pl. 30 (fig. 1)).
5. *? Crioceras deeckei* Favre (1908: 636, pl. 36 (fig. 4), pl. 37 (fig. 1), text-fig. 7).
6. *? Crioceras carinato-verrucosum* Sinzow (1905: 316, pl. 21 (figs 1–2)).
7. *Australiceras gigas* (J. de C. Sowerby) (1828: 188, pl. 593 (fig. 2)).
8. *Australiceras gigas* (Sow.) var. *anguimanum* Casey (1961: 52, pl. 13).
9. *Australiceras gigas* (Sow.) var. *arcuatum* Casey (1961: 52, pl. 12 (fig. 1a–c)).
10. *Australiceras gigas* (Sow.) var. *inscriptum* Casey (1961: 52, text-fig. 17).
11. *Australiceras? hirtzi* Collignon (1962: 19, pl. 223 (fig. 966), pl. 244 (fig. 967), pl. 225 (fig. 968)). (According to Förster 1975*a*: 57 these are actually specimens of *Ammonitoceras pavlowi* Wassiliewski, 1908.)
12. *Australiceras irregulare* (Tenison Woods) (1883: 151, pl. 8 (fig. 2)).

Fig. 49. *Australiceras robustum* Whitehouse, 1926. BMNH C25357, paratype from the Upper Aptian of Flinders River, North Queensland, Australia. × 1. (See Whitehouse 1926: 211.) According to Day (1974: 9–10) *A. robustum* may be included in the synonomy of *A. jacki.*

13. *Australiceras jacki* (Etheridge Jun.) (1880: 305, pl. 17 (figs 55–58)).
14. *Australiceras lamprum* (Etheridge Jun.) (1909: 157, pl. 48 (figs 1–2)).
15. *Australiceras laticeps* (Sinzow) (1905: 314, pl. 19 (figs 2–4)).
16. *Australiceras pingue* Casey (1961: 55, pl. 14 (fig. 1), pl. 15 (fig. 1), text-fig. 18b).
17. *Australiceras rabenjanaharyi* Collignon (1962: 26, pl. 226 (fig. 969)).
18. *Australiceras? ramboulai* Collignon (1962: 30, pl. 228 (fig. 970)). (According to Förster 1975*a*: 158–9 this is an *Ammonitoceras.*)

19. *Australiceras ramososeptatum* (Anthula) (1899: 127, pl. 14 (fig. 4)).
20. *? Crioceras sarasini* Favre (1908: 638, pl. 36 (figs 1–3), pl. 37 (fig. 2)).
21. *Australiceras tuberculatum* (Sinzow) (1905: 309, pl. 19 (figs 5–6), pl. 20 (figs 4–5)).
22. *Australiceras tuberculatum* var. *graciloides* (Sinzow) (1905: 312, pl. 20 (figs 1–3)).
23. *? Ancyloceras urbani* Neumayr & Uhlig (1881: 190, pl. 49 (fig. 3), pl. 50 (fig. 1)).

Occurrence

Australiceras occurs in the Aptian of England, France, northern Germany, Bulgaria?, the caucasian and transcaspian regions of the U.S.S.R., India, Columbia, California, Patagonia?, Australia, Madagascar, Mozambique and Zululand. Neocomian reports from Japan (Matsumoto 1947) have been disproved by Day (1969: 158). However, since then Obata *et al.* (1975) recorded *Australiceras* aff. *gigas* from the Chosi Group of Japan. Dimitrova's (1967: 62, pl. 30 (fig. 1)) *Australiceras bulgaricum* cannot be referred to the genus with certainty.

Australiceras ramososeptatum (Anthula, 1899)

Figs 50–52

Crioceras ramososeptatum Anthula, 1899: 127, pl. 14 (fig. 4). *Non* Sinzow 1905: 249, pl. 1 (figs 1–3).
Ancyloceras sp. Krenkel, 1910: 154.
Crioceras aff. *ramososeptatum:* Kasansky, 1914: 40, pl. 1 (fig. 10).
Ancyloceras ramososeptatum: Rouchadzè, 1933: 220, pl. 9 (fig. 1).
? Ammonitoceras ramososeptatum: Drushchitz & Kudryavtsev, 1960: 249, pl. 39 (fig. 1).
Toxoceratoides royerianus: Wachendorf, 1967: 290, pl. 35 (figs 1, 4, *non* fig. 5).
Australiceras ramososeptatum: Förster, 1975*a*: 153, pl. 3 (figs 1–2), text-fig. 30.

Holotype

The specimen figured by Anthula (1899, pl. 14 (fig. 4a)), here refigured as Figure 51. Original at Palaeontological Institute Uppsala University (Sjörgen Collection).

Material

SAS L7 (3) from the upper part of the section at locality 170, Mlambongwenya Creek, Zululand. Aptian I.

Description

The available specimen consists of one and a third whorls, but is sufficiently well preserved to illustrate the australiceratid characteristics. Coiling is crioceratitid with the whorls touching, but not impressed. The whorl section is subquadrate to rounded in the early stages of growth, but soon becomes triangular with a flattened dorsum, a steep umbilical wall and gently inflated flanks, converging to a rounded venter.

Fig. 50. *Australiceras ramososeptatum* (Anthula, 1899). SAS L7(3) from the upper part of the section at locality 170, Zululand, Aptian I. × 1,1.

Fig. 51. *Australiceras ramososeptatum* (Anthula, 1899). The original of Anthula's (1899, pl. 14 (fig. 4a)) *Crioceras ramososeptatum*. Housed in the Palaeontological Institute, Uppsala University (Sjörgen Coll.). Photograph supplied by Dr P. Bengtson (Uppsala). Slightly reduced.

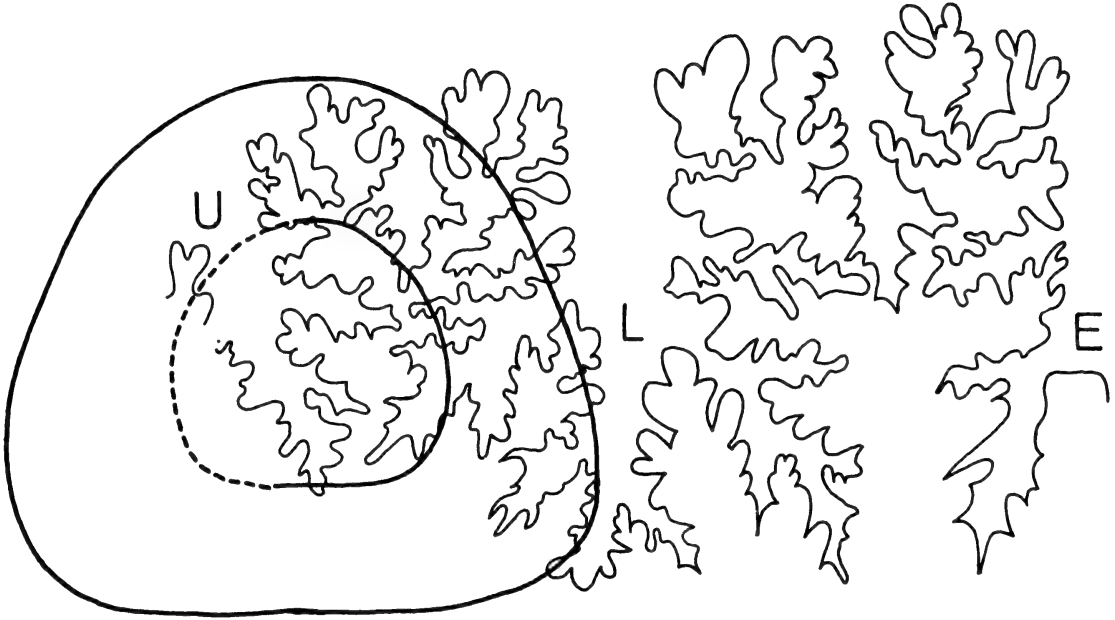


Fig. 52. *Australiceras ramososeptatum* (Anthula, 1899). SAS L3(7). Whorl section × 1 and suture line × 3.

At a whorl height of approximately 20 mm, ornament consists of alternate trituberculate ribs and non-tuberculate intermediaries. The tuberculate ribs are much stronger than the intermediaries, being about twice as wide. The ventral tubercles are largest, and situated a little distance from the siphonal line. The lateral tubercles are on the ventral third of the flanks. The umbilical tubercles are smallest and either pointed or elongated in the direction of ribbing.

After about a third of a whorl tuberculation disappears rather suddenly, and ornament consists of slightly rursiradiate ribs only, separated by interspaces of similar width. Occasional bifurcations occur at midflank.

The outer whorl is abraded and encrusted by epizoans, but appears to have borne similar ribs. The suture line is very incised, with a large asymmetrical trifid lateral lobe which covers virtually the whole of the flanks. The saddles are very narrow-stemmed.

Dimensions

Specimen	*D*	*Wb*	*Wh*	*Wb/Wh*	*U*
SAS L7 (3)	87,5	36(41,1)	36(41,1)	1	39(44,5)
	155	73(47,1)	66(42,5)	1,1	*c.* 65(41,9)

Discussion

The strong tuberculation on the inner whorl, combined with the steep umbilical wall on the outer whorl are characteristic of the species. Anthula (1899: 127) mentioned the presence of intermediary, non-tuberculate ribs which may appear regularly or sometimes be absent. This, however, does not feature prominently in Anthula's illustration or in the holotype here refigured as Figure 51.

Some subsequent references of material to Anthula's species appear to be incorrect. Sinzow's (1915, pl. 11 (figs 1–3a)) *Crioceras ramososeptatum* (especially fig. 1) has distinctly looped and ventrally bifurcating ribs, and should probably be referred to *Ammonitoceras.* The specimen figured by Drushchitz & Kudryavtsev (1960: 294, pl. 39 (fig. 1)) as *Ammonitoceras ramososeptatum* has finer ribbing than Anthula's species, and indeed appears to be *Ammonitoceras.*

Crioceras jackii Etheridge Jun. (see Figs 47–49), especially Etheridge's specimen (1909, pl. 35 (fig. 1)), is close to the present species, but differs mainly in having finer ribbing, more intermediaries during the tuberculate stage, and more bifurcating ribs in the non-tuberculate stage.

Crioceras australe Waagen *non* Moore (1875: 246, pl. 60 (fig. 1a–c)) is slightly similar, but has a rounded whorl section and a dorsal zone of impression.

Australiceras argus Anderson (1938: 211, pl. 70 (figs 1–2)) is similar in having alternate tuberculate and non-tuberculate ribs on the inner whorls, but has coarser ribbing and an ovoid whorl section on the outer whorl.

Australiceras lampros (Etheridge Jun.) has a similar triangular whorl section (see Whitehouse 1926, pl. 35 (fig. 1b)), but is only weakly trituberculate in early stages of growth.

Occurrence

Lower Aptian of southern Russia, Mozambique and Zululand.

Australiceras sp. aff. *A. irregulare* (Tenison Woods, 1883)

Figs 65C–D, 68F, 80A

Compare:

Crioceras irregulare Tenison Woods, 1883: 151, pl. 8 (fig. 2). Etheridge Jun. 1892: 501, pl. 33 (fig. 1), pl. 42 (fig. 16).

Crioceras jackii Etheridge Jun., 1909: 145 (*pars*), pl. 35 (fig. 1), pl. 36 (fig. 1), pl. 37 (fig. 2).

Australiceras irregulare: Whitehouse, 1926: 210, pl. 37 (fig. 1a–b). Day, 1974: 10, pl. 2 (fig. 3), pl. 6 (figs 1–2a–c), text-figs 3A, C. (With complete synonomy.)

Material

SAS 63/2, SAS LJE183; SAS Z8/2 from locality 168 and BMNH C79714 from locality 167, Mfongozi Creek, Aptian III–IV.

Description

A small *Australiceras*, with slightly elliptical, crioceratitid coiling. The whorls touch, but are not impressed. The whorl section is initially rounded, but progressively becomes higher than wide. The initial whorls, at a whorl height of approximately 5,5 mm, are ornamented by narrow widely spaced prorsiradiate ribs, apparently lacking tubercles. At a whorl height of approximately 7 mm, every second rib is strengthened and tubercles appear, and by a whorl height of 10 mm tuberculation is already quite prominent. The ventral tubercles are largest, and the umbilical ones smallest. The distance between the umbilical and lateral tubercles is greater than that between the latter and the ventral tubercles. The shape of tubercles is variable, the ventral ones are usually round and bullate, whereas the lateral and umbilical ones are elongated in the direction of ribbing in the early stages, but eventually also become slightly rounded. Non-tuberculate intermediaries vary from one in the initial stages to up to three, although there are normally only two in later growth stages. Ribbing is continuous, though weakened over the dorsum.

Dimensions

Specimen	*D*	*Wb*	*Wh*	*Wb/Wh*	*U*
SAS 63/2	64,6	*c.* 20(*c.* 31)	20,5(32)	*c.* 0,86	32(50)

Discussion

The scope of *Australiceras irregulare* (Tenison Woods) has been extended so far by Day (1974: 10) that the Zululand material may be tentatively referred to that species. *A. irregulare* has initial whorls with either weak or no tuberculation, and, as Day (1974, pl. 2 (fig. 3)) has shown, they are not always coiled in one plane. On the basis of the material available, a definite identification is not possible. The specimens are of some importance though, for they may point to the origin of *Helicancyloceras* gen. nov., to be described below.

Crioceras (*Ancyloceras*) *matheroni in* Pavlow (1890: 4, pl. 6 (fig. 2a–b)) bears superficial resemblance to the present species, but is too poorly known for further comment.

Occurrence

Upper Aptian of Zululand.

Australiceras wandalina (Boshoff MS.) sp. nov.

Figs 6B, 53–57, 61D

Holotype

UPG–B8 (Boshoff Collection), Department of Geology, University of Pretoria, from the Upper Aptian of Manyola Drift, northern Zululand, Aptian III. Collected by J. C. Boshoff. (Unpublished thesis 1945.)

Material

Paratype SAS EM106 is from Manyola Drift, Aptian III, Paratype BMNH C78888 is from the Upper Aptian of Mlambongwenya Spruit.

Description

The specimens are still septate at the largest diameters preserved, but judging by the rather tight coiling, it appears unlikely that the body chamber becomes detached. The initial whorl section is suboctagonal, slightly higher than wide, but eventually becomes subrectangular with a rounded venter and a slight dorsal zone of impression (Fig. 6B).

At the smallest preserved diameter (Wh = 25 mm), ornament consists of straight, radial ribs arising at the umbilical edge, each bearing three rows of pointed tubercles. The umbilical and lateral ones are situated on the dorsal and ventral thirds of the flanks respectively; the ventral ones are a little distance away from the siphonal line. All the tubercles are pointed and elongated in the direction of ribbing to a certain extent. With increasing diameter ribbing becomes blunter and the tubercles more bullate. The umbilical tubercles disappear at a diameter of *c.* 225 mm, whereas in some specimens the lateral ones, which have now migrated closer to the venter, become indistinct at a diameter of 240 mm. The ventral tubercles persist as swellings on the ventral part of the ribs to much greater a diameter.

On the inner whorl, the rib density is forty-nine per whorl and intermediaries seem to be absent. On the outer whorl, rib density is fifty-one per whorl and two intermediaries occur.

The suture line, despite decortication, appears very simple, with large and asymmetrically trifid lobes. The lateral lobe is largest and occupies virtually the whole of the flanks.

Fig. 53. *Australiceras wandalina* (Boshoff MS) sp. nov. UPG B8, holotype from Manyola Drift, Zululand, Aptian III. × 0,44.
]

Fig. 54. *Australiceras wandalina* (Boshoff MS) sp. nov. UPG B8, holotype from Manyola Drift, Zululand, Aptian III. × 0,44.

Fig. 55. *Australiceras wandalina* (Boshoff MS) sp. nov. SAS EM106 from Manyola Drift, Zululand, Aptian III. × 0,59.

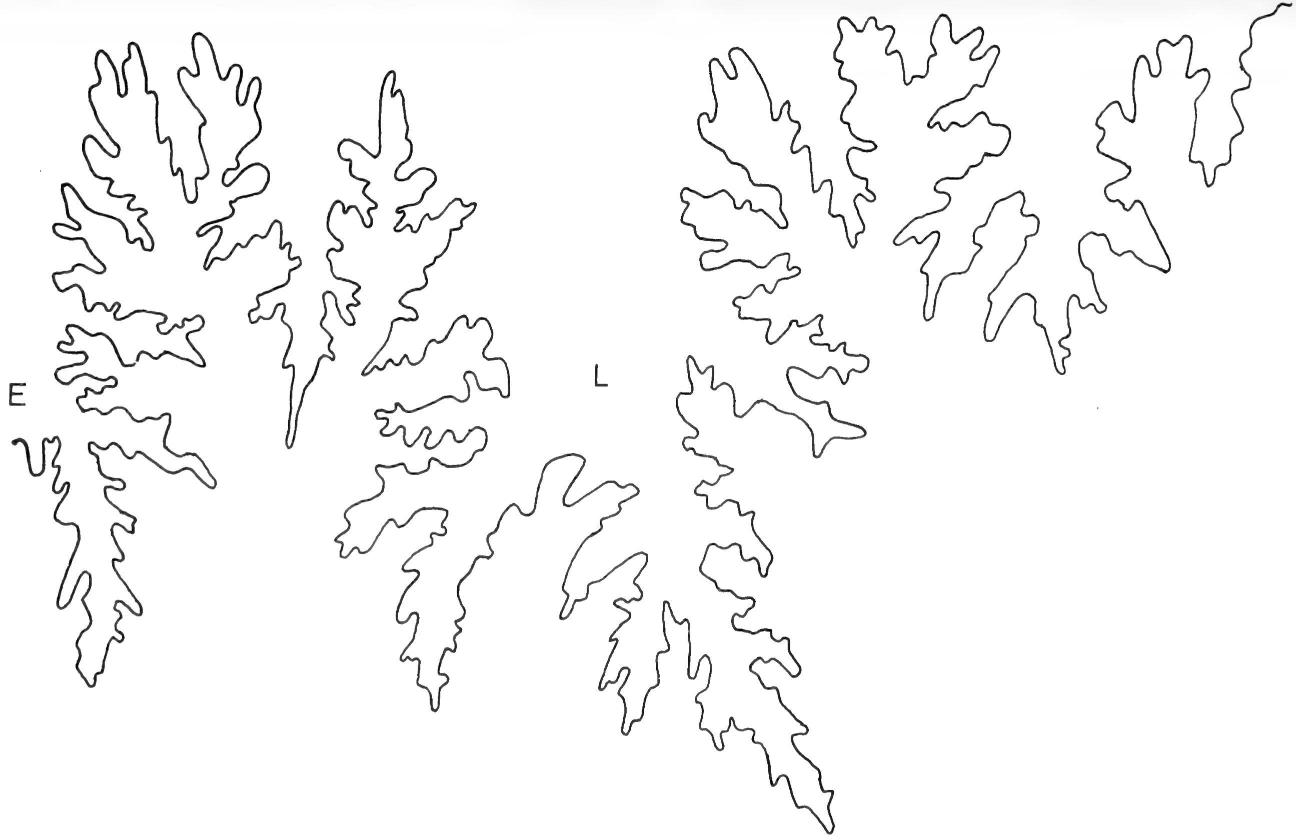


Fig. 56. *Australiceras wandalina* (Boshoff MS) sp. nov. UPG B8. Suture line × 1.

Fig. 57. *Australiceras wandalina* (Boshoff MS) sp. nov. BMNH C78888 from locality 171, Zululand. Found loose. Specimen with much finer ribbing on inner whorls, probably representing a new subspecies. × 0,67.

Dimensions

Specimen	*D*	*Wb*	*Wh*	*Wb/Wh*	*U*
UPG–B8	373	134(36)	144(38,6)	0,93	160(43)

Discussion

The strong ornamentation on the inner whorls, combined with the persistence of ventral tubercles to such a large diameter, characterize the species.

A single specimen (BMNH C78888 from locality 171 found loose on the surface (Fig. 57)) and consisting of less than half of two successive whorls has fine ribbing on the inner whorls, *c.* eighty per whorl, but ornament comparable to that of *A. wandalina* on the outer whorl, and may possibly represent a new subspecies.

Amongst Madagascan species, *Australiceras hirtzi* Collignon (1962: 19, pl. 223 (fig. 966), pl. 224 (fig. 967), pl. 225 (fig. 968)), has comparable inner whorls and relative proportions. It differs from *A. wandalina*, however, in losing its ventral tubercles at a relatively early stage, and in having finer ribbing on the outer whorl. (See Collignon 1962, pl. 225 (fig. 968).)

Australiceras rabenjanaharyi Collignon (1962: 26, pl. 226 (fig. 969)) has finer ornament both on the inner and outer whorls. *Australiceras? ramboulai* Collignon (1962: 30, pl. 228 (fig. 970)) has whorls increasing very slowly in size, and a curious ornament of ribs bifurcating from the umbilical tubercles in the later stages. As Förster (1975*a*: 158) has shown, this species is probably synonymous with *Ammonitoceras pavlowi* (Wassiliewski 1908: 46, pl. 3 (fig. 1a–c)).

Retention of tubercles to such a large diameter is reminiscent of '*Crioceras*' *deeckei* Favre (1908: 636, pl. 36 (fig. 4), pl. 37 (fig. 1), text-fig. 1) and '*Crioceras*' *sarasini* Favre (1908: 638, pl. 36 (figs 1–3), pl. 37 (fig. 2)) and the Zululand specimen to be described below as *Australiceras?* sp. cf. '*Crioceras*' *sarasini* Favre. The Patagonian species, whatever their generic identity, however, have much stronger tuberculation than the present species.

Occurrence

Upper Aptian of Zululand.

Australiceras? sp. cf. '*Crioceras*' *sarasini* Favre, 1908

Fig. 10A

Compare:

Crioceras sarasini Favre, 1908: 638, pl. 36 (figs 1–3), pl. 37 (fig. 2).

Material

SAS H71D/18 from Nhlohlela Pan, Mkuze Game Reserve, locality 150, Aptian III–IV.

Description

A small septate fragment, 130 mm long, is comparable with the larger end of the outer whorl of the original of Favre's pl. 36 (figs 1–2). The intercostal section is rounded subtriangular with a flat dorsum and moderately inflated flanks converging to a narrow venter. Maximum width is at the dorsal third of the flanks. Ornament consists of five strong, rounded, radial ribs, bearing three rows of tubercles on either side. The dorsum is smooth and devoid of ribbing. There is a distinct depression along the venter between the tubercles where ribbing is interrupted.

Discussion

As mentioned above, there is striking similarity between the Zululand specimen and the larger end of Favre's '*Crioceras*' *sarasini.* The only apparent difference is that the umbilical tubercles in the Patagonian species are larger, and that the ribs are wider spaced. However, on the basis of the limited material, a definite specific allocation is impossible. Both '*Crioceras*' *sarasini* Favre and '*Crioceras*' *deeckei* Favre are of enigmatic generic affinity. Spath erected the genus *Peltocrioceras* for '*Crioceras*' *deeckei* which 'requires a new generic designation' (Spath 1924: 85). Neither then, nor later, was any generic diagnosis given by Spath, and whether '*Crioceras*' *sarasini* was to be included in *Peltocrioceras* or not was never specified. Riccardi (1971: 277) regards both species as being representatives of *Peltocrioceras*, but as being close to both *Tropaeum* and *Australiceras.* Leanza (1963: 221) and Day (1974: 6) (the latter in comparing '*Crioceras*' *deeckei* with *Tropaeum imperator* Howchin & Whitehouse) both indirectly suggested that *Peltocrioceras* might be a junior synonym of *Tropaeum.* Wiedmann (1962: 112) regarded *Peltocrioceras* as a synonym of *Crioceratites.* '*Crioceras*' *sarasini* differs from '*Crioceras*' *deeckei* mainly in having weaker lateral tuberculation on the inner whorls, and in having interrupted ribbing over the venter, ending in strong nodes. Both species belong to the same genus, which appears to bear superficial similarity to both *Tropaeum* and *Australiceras.*

Australiceras wandalina sp. nov. is superficially similar in retaining tuberculation to large diameters, but has denser ribbing and the tubercles are not as strong.

Australiceras ramboulai Collignon (1962: 30, pl. 227 (fig. 970)) has a similar whorl section, but lacks the strong ornament.

Occurrence

'*Crioceras*' *sarasini* is of Aptian age, and not Barremian as Favre (1908) and Piatnitzky (1938) had incorrectly assumed. The Zululand specimen is of Upper Aptian age, Aptian III–IV.

Australiceras? sp. indet. A.

Fig. 38A–B

Description and discussion

A septate fragment, SAS L3 from locality 170, and of Lower Aptian age, has an octagonal whorl section and four trituberculate ribs, and is referred to

Australiceras with doubt. Ribbing is radial on the flanks, interrupted over the venter and absent on the dorsum. The fragment is possibly allied to *A. wandalina* sp. nov. and *A.* sp. cf. '*Crioceras*' *sarasini* Favre in being strongly tuberculate at large diameters.

Ammonitoceras pavlowi (Wassiliewski, 1908), described and figured from Mozambique by Förster (1975*a*: 156, pl. 3 (figs 5–7)), has a similar whorl section, but differs in having regular ventrally bifurcating or intercalatory ribs.

Australiceras? sp. indet. B.

Fig. 58A–B

Description and discussion

A curved body chamber fragment, SAS 54/45 from the Lower Aptian at locality 170 below the horizon of abundant *Ancyloceras* (*Adouliceras*) with flared, trituberculate ribs, may possibly belong to the uncoiled forms of genus *Australiceras.* The whorl section is ovoid, depressed, with a little-rounded dorsum and strongly rounded flanks and venter. Five flared ribs with distinct ventral but indistinct lateral and umbilical tubercles are present. The dorsum is ornamented by faint striae.

The strongly depressed whorl section recalls Sinzow's *Crioceras laticeps* (1905: 314, text-fig. 3, pl. 19 (figs 2–4)). In Sinzow's species, however, rib density is less than in the present specimen. Specimens of *Australiceras gigas* (J. de C. Sowerby) sometimes also show such flared ribs in the crozier, but again, the rib density is lower.

Subfamily Helicancylinae Hyatt, 1894

Hyatt's family Helicancylidae was revived by Casey (1961: 76, as Helicancylinae) 'as a useful subfamily term for those diminutive ancyloceratids in which the sculpture is simplified on the terminal hook'.

The subfamily, as interpreted by Casey, is here accepted with reservation as a useful grouping of three genera only: *Tonohamites* Spath, 1924, *Toxoceratoides* Spath, 1924, and *Helicancylus* Gabb, 1869, although *Acrioceras* Hyatt, 1900, *Lytocrioceras* Spath, 1924, and *Leptoceras* Uhlig 1883, have also tentatively been referred to the sub-family.

Apart from the fact that the type genus is difficult to interpret (see Casey 1961: 77), transitional forms occur, linking the genera. Classification is based mainly on the mode of ribbing on the body chamber and, to a lesser extent, the presence or absence of (tri-)tuberculation on the phragmocone.

Genus *Toxoceratoides* Spath, 1924

Type species

Toxoceras royerianum d'Orbigny, 1842 from the Lower Aptian of France.

Fig. 58. *Australiceras?* sp. ind. B. SAS 54/45 from locality 170, Zululand, Aptian I. × 1.

Diagnosis

Small forms with ancyloceratid or leptoceratid coiling, probably with an initial helix. Trituberculate ribs occur on the phragmocone but disappear on the recurved hook.

Discussion

The genus was discussed extensively by Casey (1961: 79) and little can be added. Differences between *Toxoceratoides* and *Tonohamites* are slight, and trituberculate forms such as *Tonohamites decurrens* connect the two genera.

The following species were referred to genus *Toxoceratoides* by Casey (1961):

1. *Toxoceratoides biplex* (von Koenen) (1902: 381, pl. 41 (figs 3, 10a–b, 11a–b).
2. *Toxoceratoides caucasicus* (Kasansky) (1914, pl. 1 (fig. 8a–c)).
3. *Toxoceratoides fustiformis* (von Koenen) (1902: 384, pl. 41 (figs 4–5, 7a–c, 9a–b), pl. 53 (figs 8a–b, 9a–b)).
4. *Toxoceratoides obliquatus* (Young & Bird) (1828: 278, pl. 18 (fig. 11).
5. *Toxoceratoides proteus* (Spath) (1930: 461, pl. 16 (fig. 7)).
6. *Toxoceratoides rochi* Casey, 1961 (=*Ancyloceras royerianum in* Roch 1927: 30, pl. 1 (fig. 4)).
7. *Toxoceratoides rotundus* (Phillips) (1875: 264, pl. 1 (fig. 24)).
8. *Toxoceratoides royerianum* (d'Orbigny) (1842: 481, pl. 118 (figs 7–11)).
9. *Toxoceratoides seminodosus* (Roemer) 1841.
10. *Toxoceratoides sheperdi* (Spath) (1942: 173, figs 5–6).

To this list may be added:

11. *Toxoceratoides biplicatum* (von Koenen) (1902: 379, pl. 41 (figs 2a–b, 8a–b)).
12. *Toxoceratoides krenkeli* Förster (1975a: 160, pl. 4 (figs 1–2), text-fig. 33a–b).
13. *Toxoceratoides saulae* Murphy (1975: 31, pl. 4 (figs 4, 6)).
14. *Toxoceratoides starrkingi* (Anderson) (See Murphy 1975: 32, pl. 4 (figs 3, 5)).
15. *Toxoceratoides corae* Murphy (1975: 33, pl. 5 (figs 1, 5)).
16. *? Toxoceratoides greeni* Murphy (1975: 33, pl. 5 (figs 2–3, 6)).
17. *Toxoceratoides* spp. indet. described by Murphy as *Toxoceratoides* sp. 1 (1975: 35, pl. 6 (figs 1–2, 11) and *?Toxoceratoides* sp. (1975: 35, pl. 3 (fig. 6), pl. 6 (figs 5–6)).
18. *Toxoceratoides* sp. nov. Thomson (1974: 16, pl. 3a, d).

Occurrence

Toxoceratoides ranges from the Upper Barremian to Upper Aptian, and is known from Europe, California and south-east Africa. Reports from Australia are not accepted here. '*Ancyloceras*' *taylori* Etheridge, referred to *Toxoceratoides* by Whitehouse (1926: 216) is a doubtful contender, as are the five specimens described by Day (1974: 13) as *Toxoceratoides?* spp.

Toxoceratoides royerianus (d'Orbigny, 1842)

Fig. 59E

Toxoceras royerianus d'Orbigny, 1842: 481, pl. 118 (figs 7–11).
? Toxoceras emericianus d'Orbigny, 1842: 487, pl. 120 (figs 5–9).
Toxoceratoides royerianus: Casey, 1961: 78, pl. 6 (fig. 2a–b), pl. 17 (fig. 3a–b), text-fig. 30a–h) (cum synon.).

Neotype

The specimen figured in Casey (1961, text-fig. 30a–c) from the Lower Aptian of Haute Marne, France, and in the collections of the Sorbonne, Paris.

Material

SAM–PCM5313 from Lubemba, southern Mozambique.

Description

A recurved crozier with part of the phragmocone is referred to the species.

The part of the phragmocone preserved on the recurved crozier is heavily abraded and only umbilical tubercles are preserved. At the apertural end of the crozier the whorl section is ovoid, with a flattened dorsum, sharp umbilical edge and broadly rounded venter. Ornament consists of relatively narrow, high ribs, separated by deep interspaces which are wider than the ribs. The ribs arise in groups of two or three from the umbilical tubercles. They are prorsiradiate at the proximal end of the crozier, but become radial on the bend of the crozier and at the distal end. At the apertural end a pair of single ribs arises from the umbilical tubercles.

Discussion

The recurved crozier compares well with the illustrations and figures provided by Casey (1961), who also discussed the species extensively.

Toxoceratoides krenkeli Förster, 1975*a* differs from *T. royerianus* mainly in having hardly any intermediary ribs on the shaft, and in having coarser ribbing on the crozier.

Occurrence

Lower Aptian of western and central Europe, Mozambique and Zululand.

Toxoceratoides krenkeli Förster, 1975

Fig. 59F

Hamites royerianus: Kilian, 1902: 465.
Ancyloceras royerianum: Krenkel, 1910: 151, pl. 17 (figs 12–13).
Tonohamites royerianum: Haughton & Boshoff, 1956: 13, pl. 2 (fig. 3).
Acrioceras dissimilis: Wachendorf, 1967: 281, pl. 35 (figs 2–3), text-fig. 5.
Toxoceratoides royerianus: Wachendorf, 1967: 290, pl. 35 (fig. 5, *non* figs 1, 4).
Toxoceratoides krenkeli Förster, 1975*a*: 160, pl. 4 (figs 1–2) text-fig. 33a–b.

Holotype

Wachendorf's (1967, pl. 35 (fig. 2)) specimen from Chalala, Mozambique.

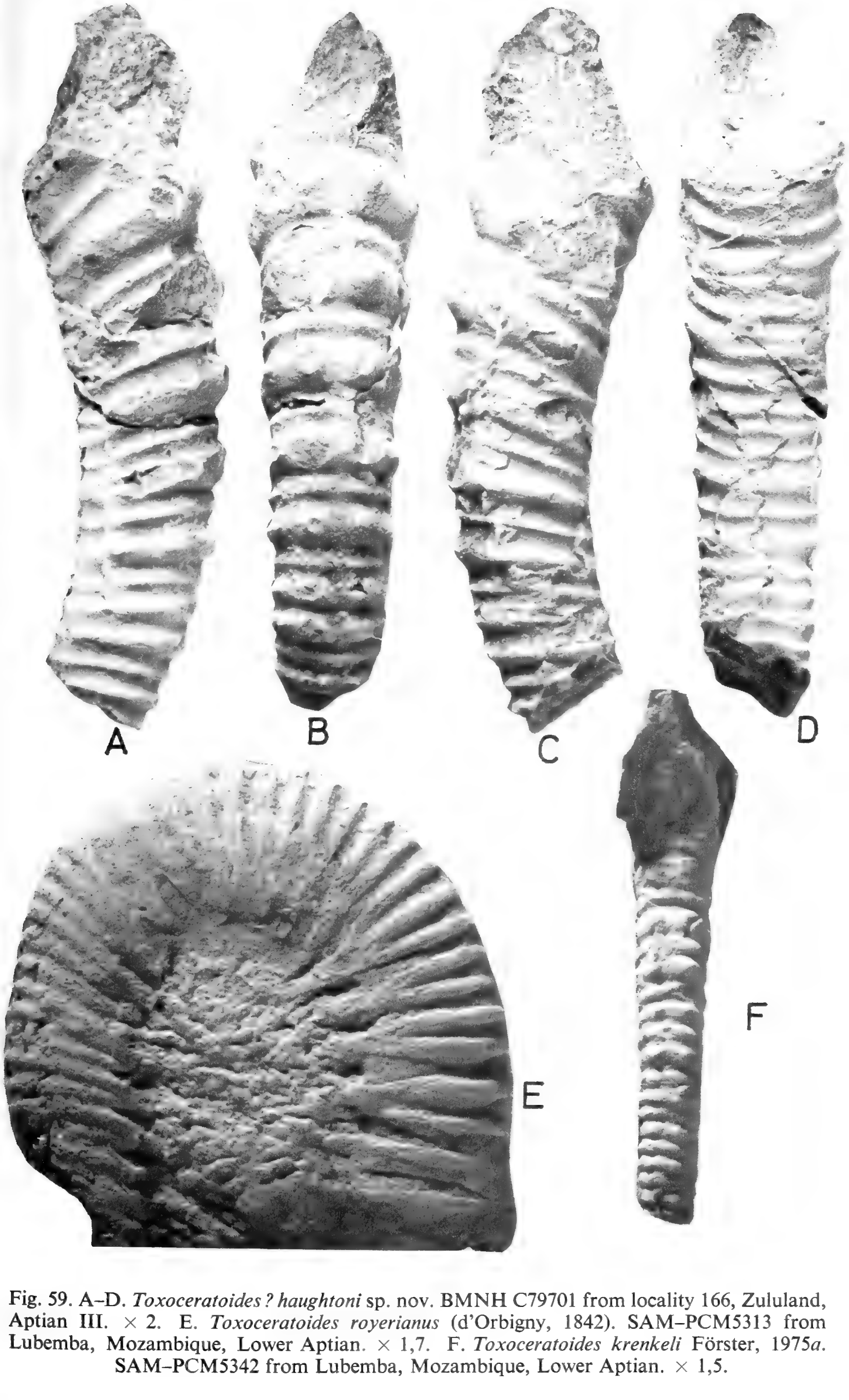


Fig. 59. A–D. *Toxoceratoides? haughtoni* sp. nov. BMNH C79701 from locality 166, Zululand, Aptian III. × 2. E. *Toxoceratoides royerianus* (d'Orbigny, 1842). SAM–PCM5313 from Lubemba, Mozambique, Lower Aptian. × 1,7. F. *Toxoceratoides krenkeli* Förster, 1975*a*. SAM–PCM5342 from Lubemba, Mozambique, Lower Aptian. × 1,5.

Material

SAM–PCM5342 from Lubemba, southern Mozambique, Lower Aptian.

Description and discussion

A small, slightly curved part of the phragmocone is referred to Förster's species.

The whorl section is nearly circular on the earliest part preserved. Up to a diameter of 5,5 mm ornament consists of strongly prorsiradiate ribs, separated by interspaces of similar width. Rib density is about four per whorl height. The ribs weaken markedly on, and pass straight across the dorsum. Tuberculation commences at a diameter of 5,5 mm; at first only ventral tubercles are present, but four ribs further on, distinct, though small lateral and umbilical tubercles are present, and there are faint indications of duplication of ribs over the dorsum.

Förster (1975*a*: 160 *et seq.*) discussed the affinities of the species in detail; its main characteristic is the sparsity or absence of non-tuberculate intercalatories on the shaft. The present specimen adds to our knowledge of the species in that it illustrates that the early parts of the curved shaft lack tubercles; in this respect it resembles the later *Toxoceratoides? haughtoni* sp. nov. of Late Aptian age, described below.

Occurrence

Lower Aptian of southern Mozambique.

Toxoceratoides? haughtoni sp. nov.

Figs 59A–D, 60A–I, 61A–C, 62A–D, 63, 64A–C, 65A–B, 66B, 79A–B

Holotype

SAS 64/T1 from locality 168, Mfongozi Creek, northern Zululand. Aptian III–IV. South African Geological Survey Collection, Pretoria. Collected by H. Klinger 1970.

Derivation of name

The species is named in honour of Dr S. H. Haughton, discoverer of many Cretaceous localities in northern Zululand.

Material

Apart from the holotype, SAS L65/T2, SAS Z8/T1, SAS Z8/T4, SAS Z8/T5, SAS LJE 186, all from locality 168, Mfongozi Creek, Zululand, and BMNH C79690, C79191, C79694–79701 from locality 166, Aptian III, Aptian III–IV, and SAS N2 from locality 50.

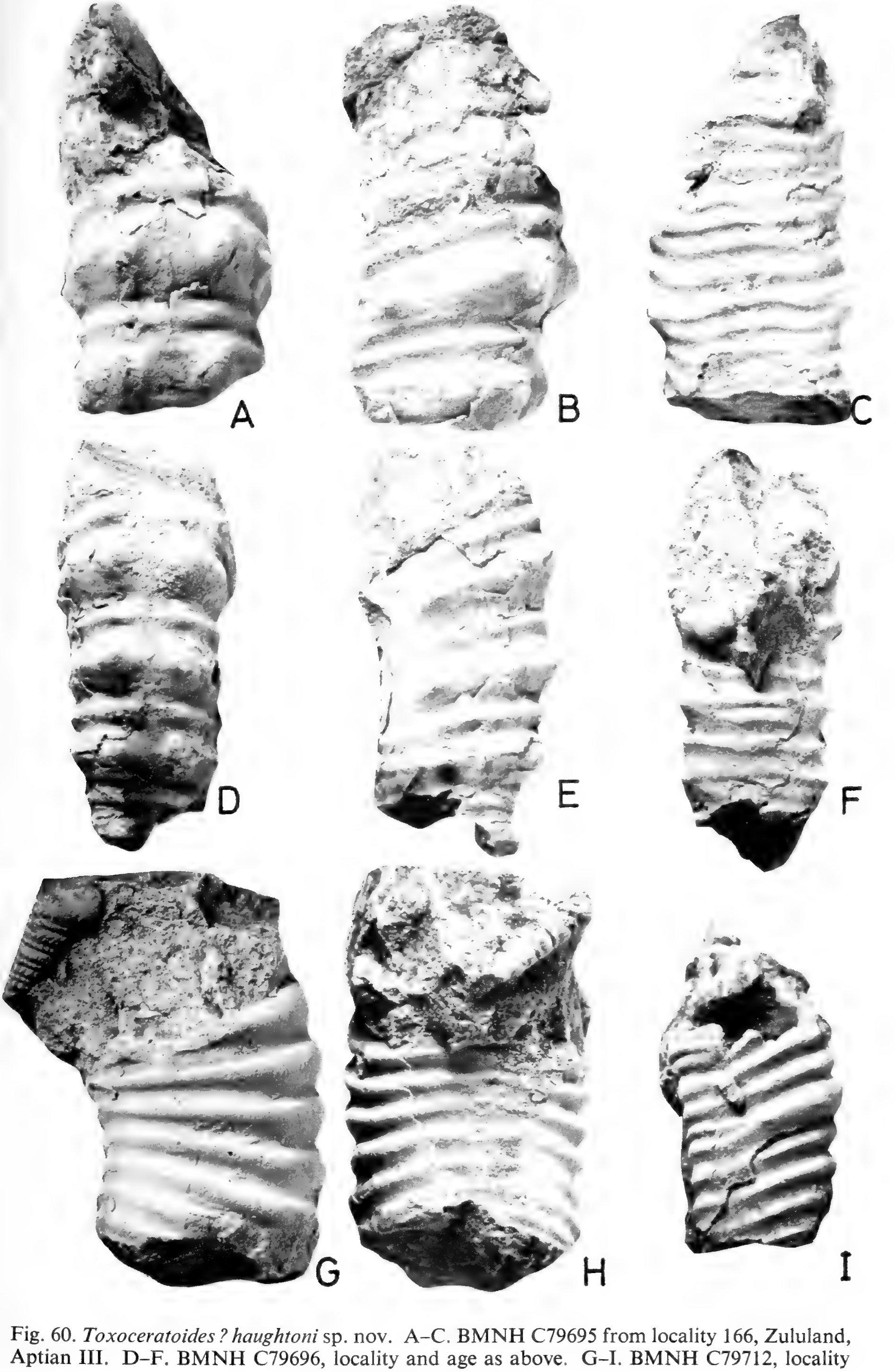


Fig. 60. *Toxoceratoides ? haughtoni* sp. nov. A–C. BMNH C79695 from locality 166, Zululand, Aptian III. D–F. BMNH C79696, locality and age as above. G–I. BMNH C79712, locality and age as above. All × 2.

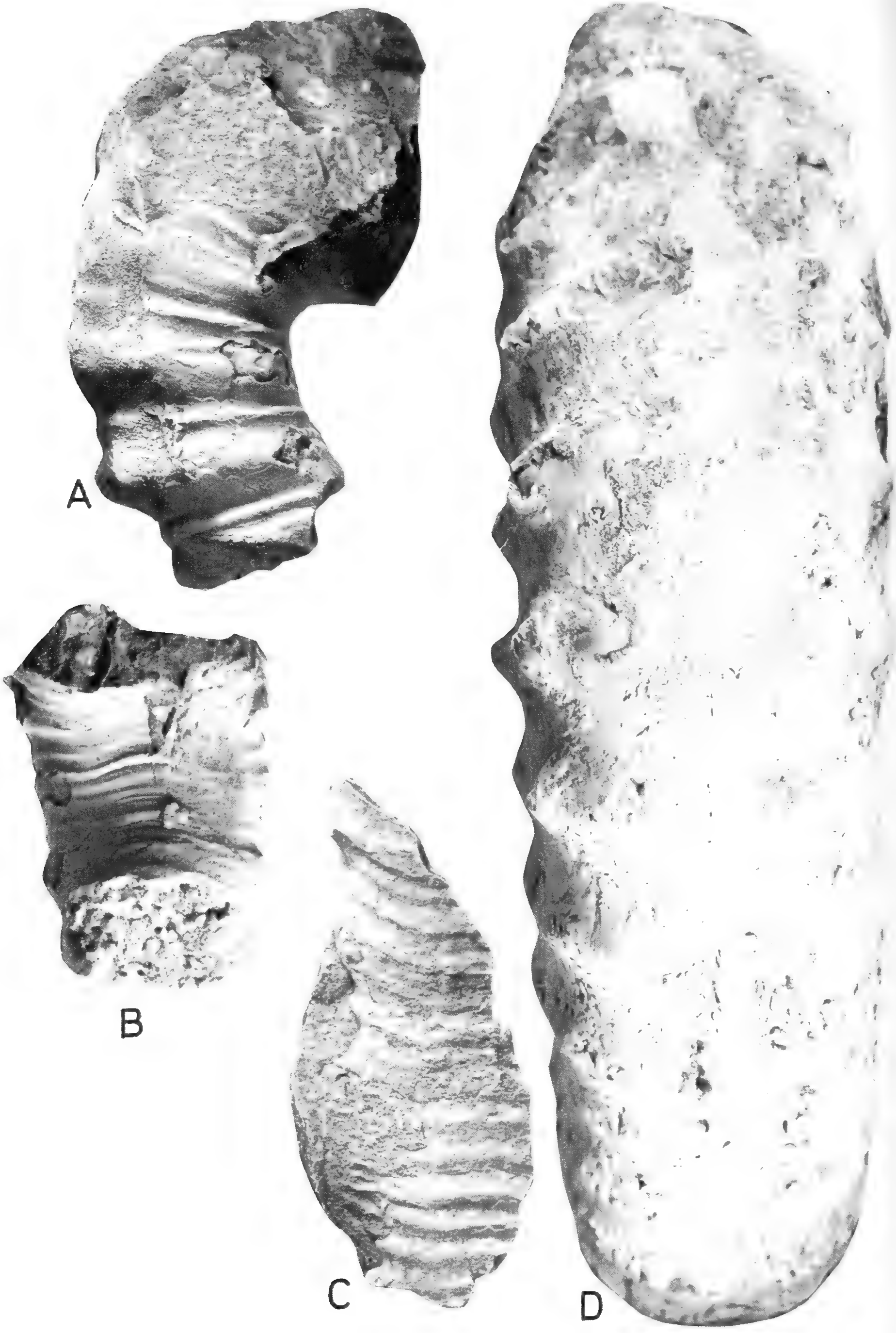


Fig. 61. A–C. *Toxoceratoides? haughtoni* sp. nov. BMNH C79694 from locality 166, Zululand, Aptian III. × 2. D. *Australiceras wandalina* (Boshoff MS) sp. nov. BMNH C7888 from locality 171, Zululand. Aptian. × 0,67.

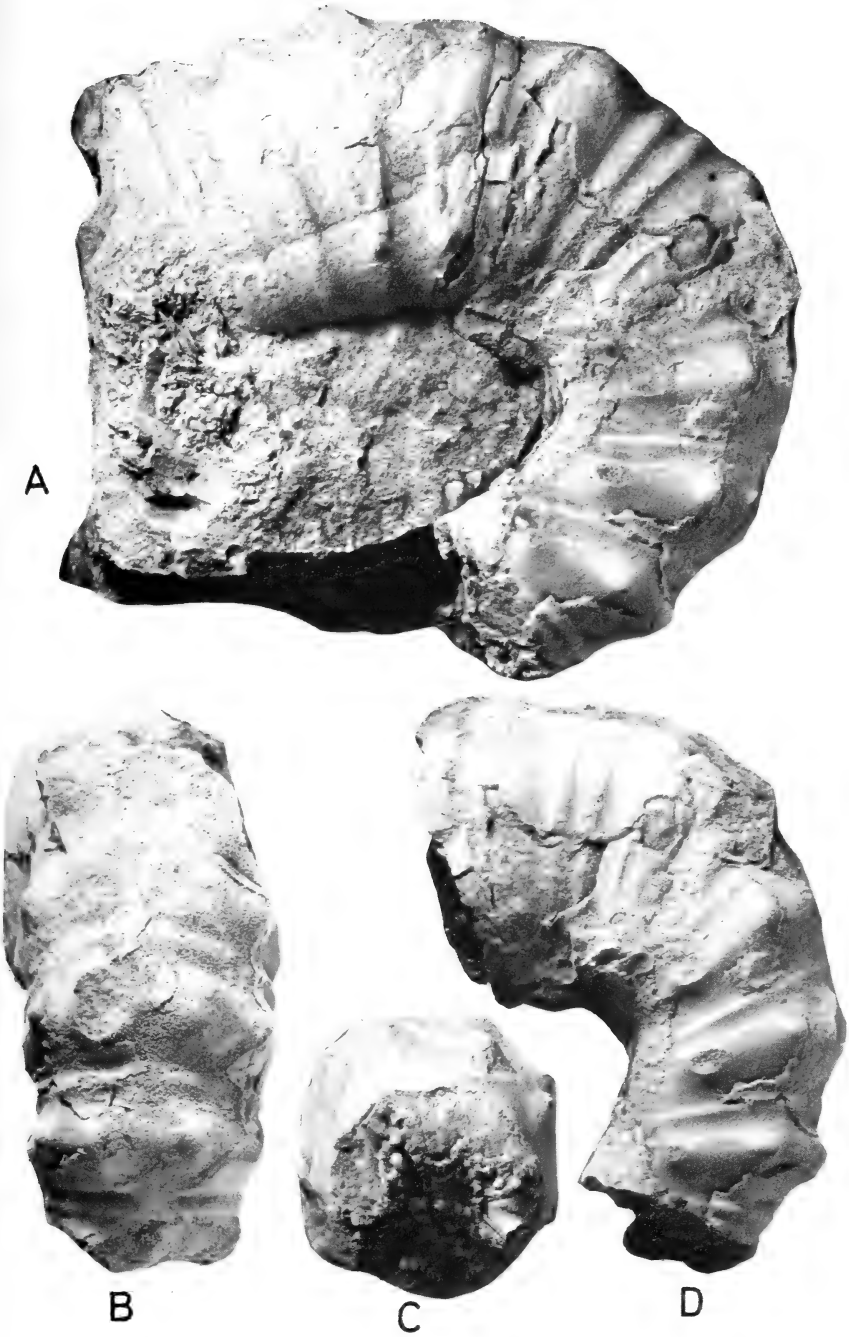


Fig. 62 A–D. *Toxoceratoides ? haughtoni* sp. nov. BMNH C79694 from locality 166, Zululand, Aptian III. × 2.

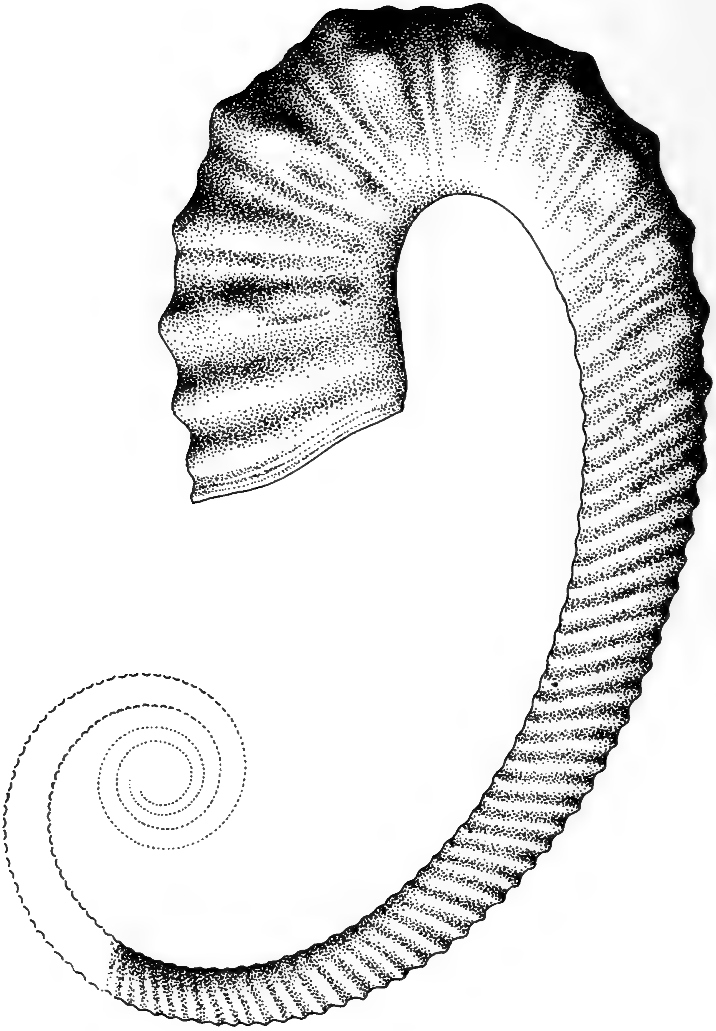


Fig. 63. Diagrammatic reconstruction of *Toxoceratoides? haughtoni* sp. nov.

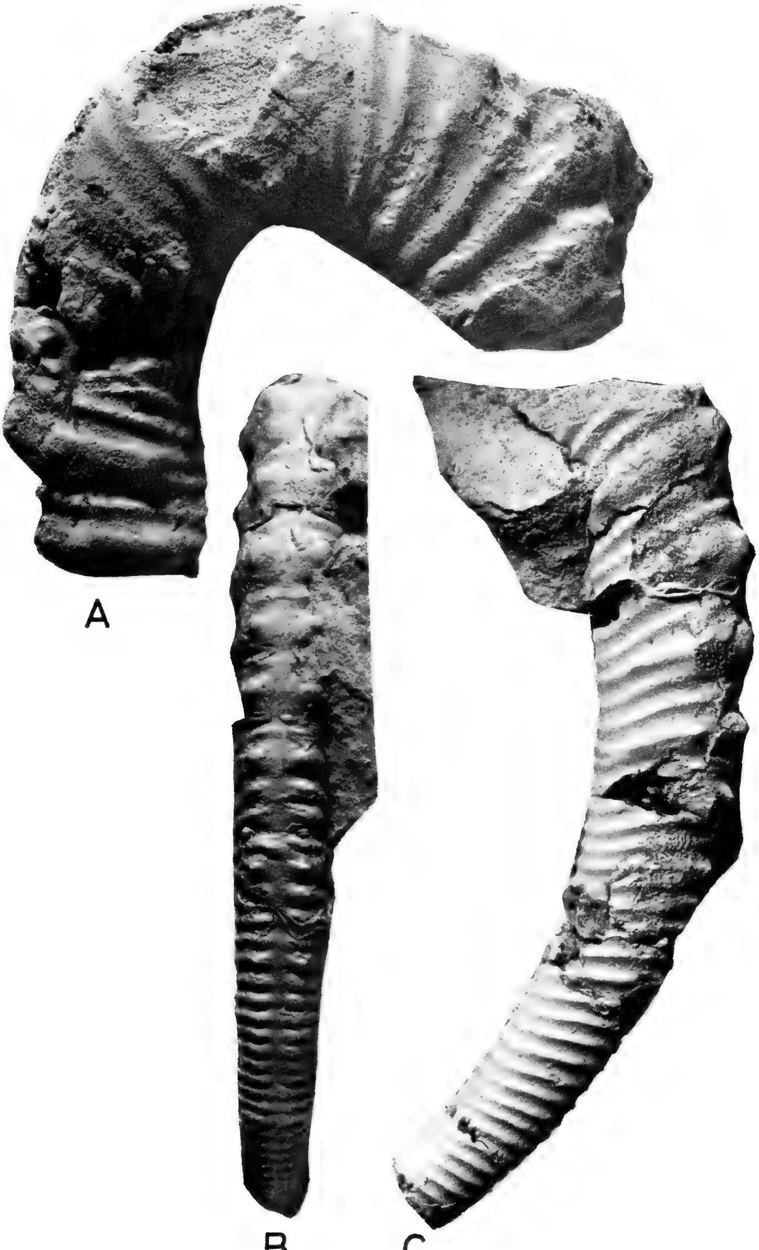


Fig. 64. *Toxoceratoides ? haughtoni* sp. nov. A. SAS Nd from locality 50, Upper Aptian. × 1,6. B–C. SAS 64/T1, holotype from locality 168, Zululand, Aptian III–IV. × 1,4.

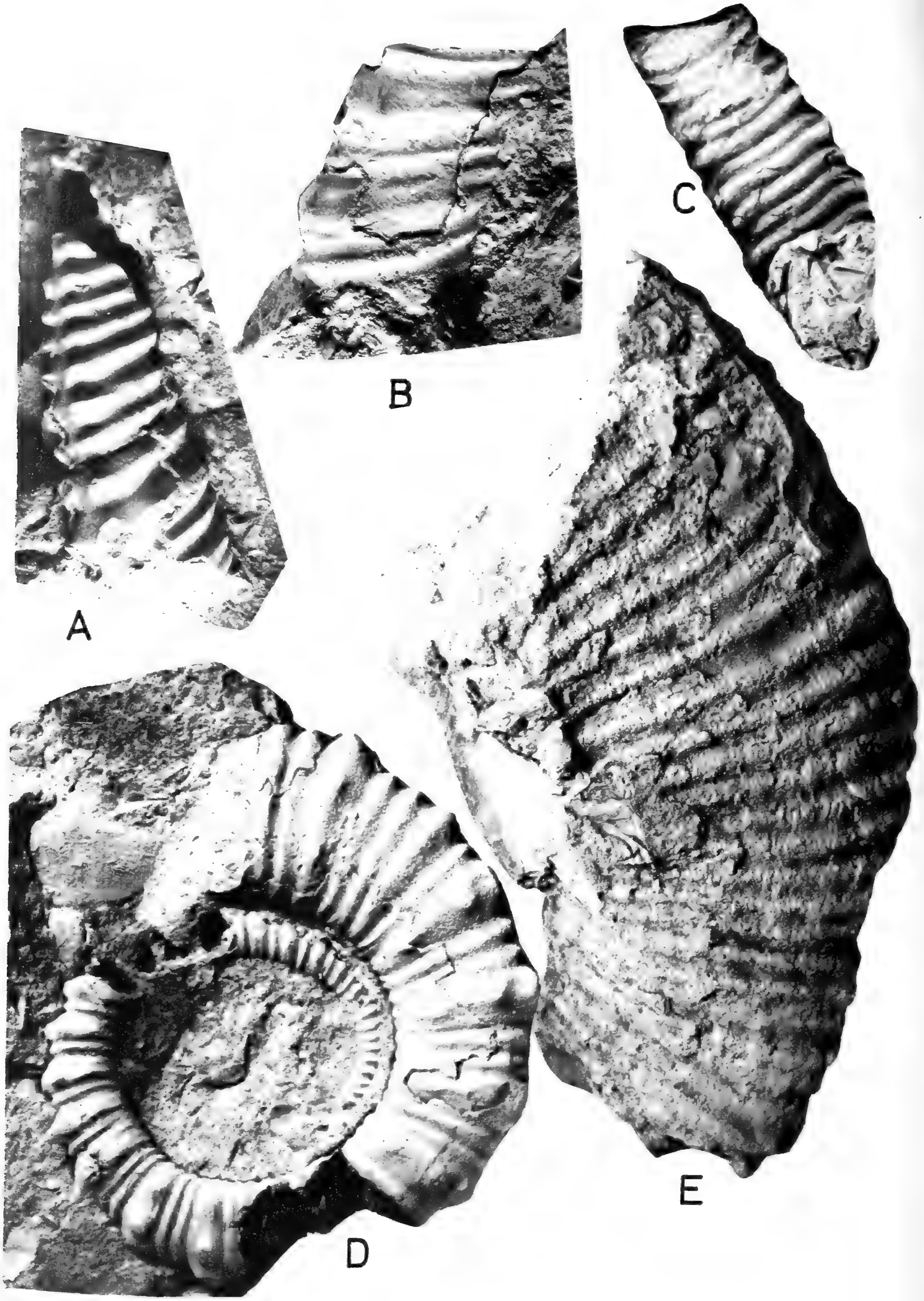


Fig. 65. A–B. *Toxoceratoides ? haughtoni* sp. nov. A. SAS LJE 186 from locality 168, Zululand, Aptian III–IV. × 1,5. B. SAS Z8/T5 from locality 168, Zululand, Aptian III–IV. × 1,5. C–D. *Australiceras* sp. aff. *irregulare*. C. SAS Z8/T5a from locality 168, Aptian III–IV. × 1,5. D. SAS L65/2 from locality 168, Zululand, Aptian III–IV. × 1. E. *Tropaeum obesum* sp. nov. SAM–PCZ5681. Fragment of inner whorl of holotype. × 1.

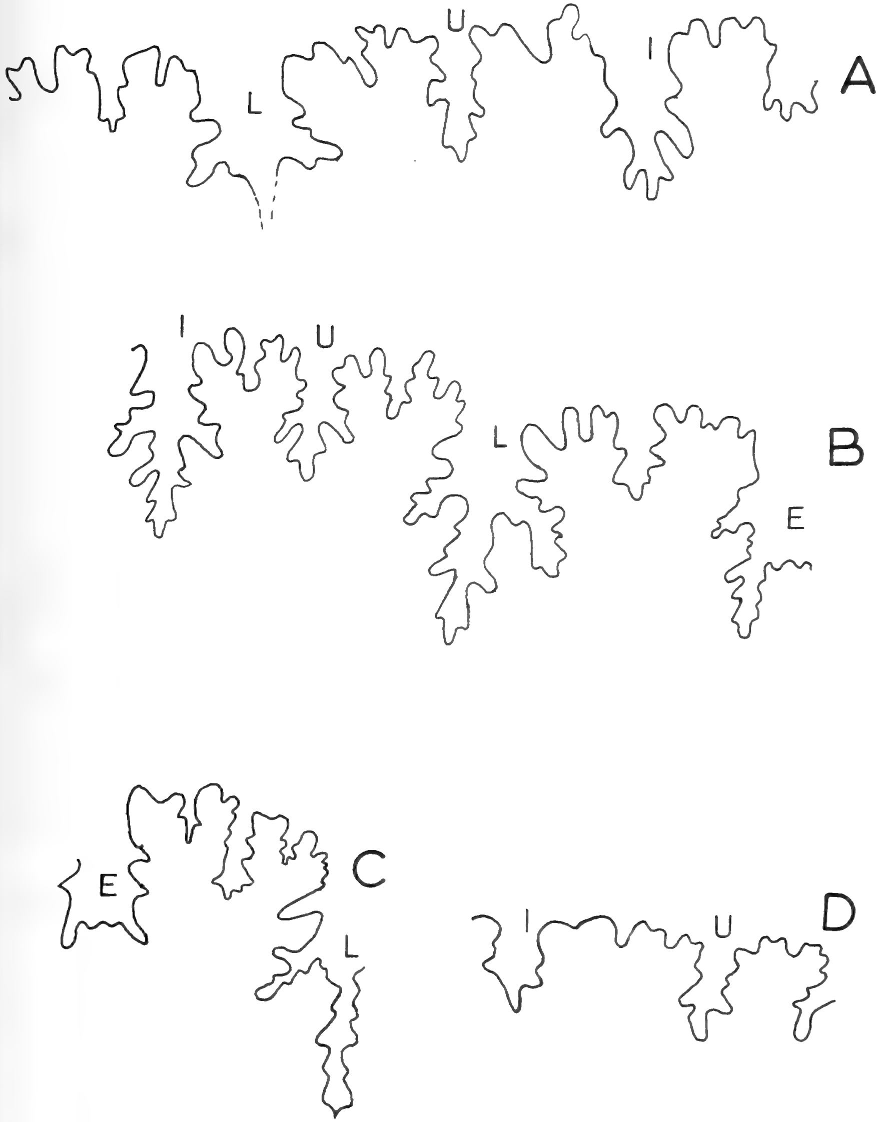


Fig. 66. A. Suture line of *Tonohamites koeneni* Casey, 1961. SAS Z1115 at diameter *c.* 8 mm. × 6. B. Suture line of *Toxoceratoides? haughtoni* sp. nov. at diameter *c.* 8 mm. × 6. C–D. Suture lines of *Tonohamites koeneni* Casey, 1961. C. SAS Z1115 at diameter *c.* 15 mm. × 3. D. SAS H71D/19 at diameter *c.* 16 mm. × 3.

Description

The coiling is toxoceratoid, open with a recurved crozier. The very early stage of growth is unknown. The whorl section is initially rounded, but becomes laterally compressed as size increases. Ornamentation is best shown by the holotype. At the smallest diameter, 6,1 mm, ornament consists of single, simple ribs, slightly prorsiradiate and separated by interspaces of similar width. At this stage there are approximately six ribs in a distance equal to the whorl diameter. At a slightly larger diameter the ribs become increasingly differentiated over the venter. Initially this appears as a mere flattening along the siphonal line, but at larger diameters the ribs are distinctly interrupted over the venter, terminating in small tubercles on either side of the siphonal line. Initially, all the tubercles are of equal size, but at a diameter of 8,5 mm some appear stronger than the others. With increasing diameter, these tubercles appear with greater frequency and become greatly enlarged, whilst the ribs on which they are situated become bolder on the flanks, and small ventrolateral and even smaller umbilical tubercles appear on the ventral and dorsal thirds of the flanks respectively. One (or rarely two) intermediate non-tuberculate ribs are present. At large diameters, the ribs connecting the ventral and ventro-lateral tubercles may become flattened, or even show signs of looping, in a manner reminiscent of some *Protanisoceras* species.

Ribbing weakens on the dorsum, and the ribs pass straight across or have a slight forward curvature. Some of the major ribs show distinct looping or duplication on the dorsum.

Ornament remains more or less constant up to the sharply recurved crozier. In the bend of the crozier more intercalated, thin ribs occur, and on the recurving limb all ornament, with the possible exception of the ventral tubercle, weakens.

The suture is relatively symmetrical with a trifid lateral, umbilical and internal lobe.

Discussion

All the available specimens show toxoceratoid coiling. If this species is a true *Toxoceratoides*, it extends the range of the genus to the Upper Aptian. The peculiar ornament in the early whorls and the lack of regular simple ribbing in the crozier is different from that of the normal *Toxoceratoides* ornament, hence the species is referred to this genus with doubt. This also serves to distinguish it from all the other known species of *Toxoceratoides*.

The non-tuberculate ribbed stage is comparable to that of *T. krenkeli*. That species, however, is tuberculate at much smaller diameters and has a depressed whorl section, different from the compressed whorl of *T. ? haughtoni*.

Ancyloceras patagonicum Stolley (1912: 11, pl. 1 (figs 2a–b, 3a–b)) may also be compared with the present species. The Patagonian species has, however, stronger ribbing in the early stages of growth, whilst the major costae are not as strongly developed as in the present species.

One of Von Koenen's specimens of *Ancyloceras fustiforme* (1902, pl. 53 (fig. 9)) bears some resemblance to the early parts of *T.? haughtoni* in having ventrally differentiated ribbing which becomes tuberculate with increasing diameter. In later stages, however, this species is not as strongly tuberculate as the Zululand material, as is illustrated by the original of Von Koenen's (pl. 41, fig. 9) specimen.

Occurrence

Fairly common in the Upper Aptian of Zululand.

Genus *Tonohamites* Spath, 1924

Type species

Tonohamites decurrens Spath, 1924 from the Lower Aptian of Ahaus, Germany, by original designation.

Diagnosis

Coiling labeceratid. Tuberculation weaker than in *Toxoceratoides* and mostly confined to the venter. Ribbing in early stages hamitid, but towards body chamber broad and flat in some.

Discussion

Like *Toxoceratoides*, *Tonohamites* was doubtfully regarded as a synonym of *Hamiticeras* by Wright (1957: L212). Casey (1961: 84), however, maintains that it is quite a valid and useful genus for small labeceratid-like forms with reduced tuberculation on the phragmocone and rounded ribbing on the venter. *Tonohamites decurrens* Spath with strong trituberculation on the phragmocone connects *Tonohamites* with *Toxoceratoides*, thus illustrating the close relationship between the two genera.

The genus was discussed at length by Casey (1961: 84) and, apart from extending the stratigraphic and geographical range of the genus, no further comments are necessary.

Species referred to *Tonohamites* by Casey are as follows:

1. *Tonohamites decurrens* Spath, 1924: 461. (Lectotype is Von Koenen's 1902, pl. 33 (fig. 2) and lower part of pl. 33 (fig. 3)).
2. *Tonohamites aequicingulatus* (von Koenen) (1902: 394, pl. 37 (figs 5a–c, 6a–e)).
3. *Tonohamites? eichwaldi* (Jasykow) *in* Sinzow (1872: 36, pl. 6 (figs 7–9)).
4. *Tonohamites? hunstantonensis* Casey (1961: 90, pl. 21 (fig. 1a–d)).
5. *Tonohamites koeneni* Casey: (1961: 89). Holotype is Von Koenen's (1902, pl. 33 (fig. 3a)) specimen, upper part only.
6. *Tonohamites limbatus* Casey (1961: 89, pl. 22 (figs 3a–c, 4), pl. 21 (fig. 3a–b)).
7. *Tonohamites? undosus* (von Koenen) (1902: 393, pl. 35 (fig. 13a–f)).

Occurrence

Tonohamites occurs in the Lower Aptian of Europe and the Upper Aptian of Madagascar and Zululand.

Tonohamites koeneni Casey, 1961

Figs 66A, C–D, 67C–D, 73A, 81F

Hamites decurrens (*non* Roemer) von Koenen, 1902: 392, pl. 33 (fig. 3a upper part only).
Tonohamites koeneni: Casey, 1961: 89, text-fig. 35g–h.

Holotype

The top part only of the specimen figured by Von Koenen (1902, pl. 33 (fig. 3)) as *Hamites decurrens* by original designation (Casey 1961: 89).

Material

SAS Z1115, SAS Z1118, SAS H71D/19 all from locality 152, Mkuze Game Reserve. Aptian IV.

Description

The most complete specimen, SAS Z1115 (Fig. 67C–D), shows the coiling to be labeceratid, with a moderately long shaft. Coiling of the very early whorls is unknown.

The whorl section is rounded in the early whorls, but becomes progressively flattened dorsoventrally with a nearly flat dorsum. Maximum width is at midflank or just dorsal to it. Ornament on the curved shaft consists of simple, prorsiradiate ribs, separated by narrower interspaces. The ribs are narrow on the dorsum and nearly radial, then are prorsiradiate and cross the flank with increasing strength. Towards the venter the ribs become more rounded and wider, a tendency which is especially pronounced on the body chamber. There are four to four and a half ribs in a distance equal to the whorl diameter on the shaft. At the bend on the crozier, the ribs become extremely flattened on the venter and the interspaces on the flanks become wider. The aperture appears to be quite simple, with neither lappets nor a constriction.

Discussion

As Casey (1961: 84) has outlined, Von Koenen's illustration of *Hamites decurrens* (1902, pl. 33 (figs 2, 3a–b)) is a synthetograph. The lower part of the synthetograph was chosen by Casey as lectotype of *Tonohamites decurrens* Spath, whilst the upper part was regarded as a new species, *Tonohamites koeneni.* The Zululand material fits the upper part of Von Koenen's figure so well that the authors have no hesitation in referring it to *T. koeneni*, despite differences in age. *T. koeneni* is believed to be of Lower Aptian age (as is the whole genus in the sense used by Casey (1961: 85)). The Zululand material is of Upper Aptian age, occurring just below the line of hiatus concretions (Kennedy & Klinger 1972) marking the Aptian/Albian boundary.

Casey's *Tonohamites* cf. *koeneni* (1961: 89, pl. 20 (fig. 5a–b)) from the Lower Aptian of Kent does not show as pronounced broad flattened ribs on the body chamber as do Von Koenen's or the Zululand specimens.

Tonohamites decurrens Spath has a distinct trituberculate phragmocone,

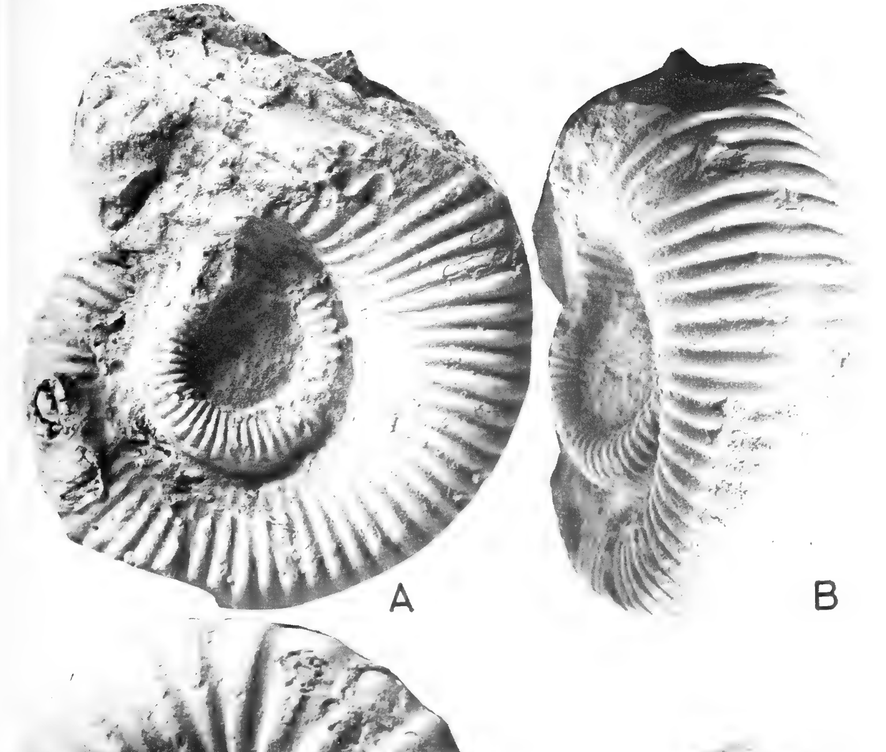


Fig. 67. A–B. *Helicancyloceras* (*Helicancyloceras*) *densecostatum* sp. nov. SAM–PCZ5682, holotype from locality 168, Zululand, Aptian III–IV. × 1,3. C–D. *Tonohamites koeneni* Casey, 1961. SAS Z1115 from locality 152, Zululand, Aptian IV. × 1,4.

and is easily distinguished. *T. aequicingulatus* (von Koenen) has a somewhat similar body chamber, but has ventral tubercles on the shaft. *T. limbatus* Casey has a long, descending limb and small tubercles on the phragmocone.

Occurrence

Upper Aptian of Zululand. The English specimen tentatively referred to the species by Casey is from the Lower Aptian *bowerbanki* Zone. In Germany the species occurs in the Lower Aptian of Ahaus.

Tonohamites aequicingulatus (von Koenen, 1902)

Figs 68A–E, 38C, 88D

Hamites aequicingulatus von Koenen, 1902: 394, pl. 37 (figs 5–6).
Tonohamites aequicingulatus Casey, 1961: 87, pl. 9 (figs 2a–b, 3a–b, 4), text-fig. 32.
Tonohamites sp. aff. *aequicingulatus* Collignon, 1962: 14, pl. 221, (fig. 970).

Lectotype

The original of Von Koenen (1902, pl. 37 (fig. 5a–c)) by subsequent designation Casey 1961: 87.

Material

SAS Z8Ta1 from locality 168, BMNH C79690, C79692 from locality 166, Mfongozi Creek, Zululand. Aptian III–IV.

Description

The available specimens are fragmentary and consist of slightly curved shafts. The whorl section is depressed, with rounded flanks and a flattened dorsum and venter.

Ornament consists of prominent, obliquely prorsiradiate ribs, separated by wider interspaces. The ribs are strongest on the flanks, thickening towards the ventrolateral region. In the siphonal area the ribs are interrupted or weakened at the larger diameter. At the smaller ends of the shaft there is no distinct weakening of ribbing over the venter. The ribs pass radially or with a slight forward curvature over the dorsum.

Discussion

T. aequicingulatus presents difficulties in interpretation, as it is only known from fragments, and, as Casey (1961: 88) noted, it 'seems practicable to treat these fragments as belonging to a single, variable species'.

The Madagascan specimen tentatively referred to this species by Collignon has a rib density of four or five per diameter, the general appearance being similar to that of the Zululand material, and it is probably conspecific. The only apparent difference between the figured European specimens in Casey (1961) and Von Koenen (1902) and those from Zululand and Madagascar, is that the ribbing in the latter specimens is stouter near the venter. The subsymmetrical

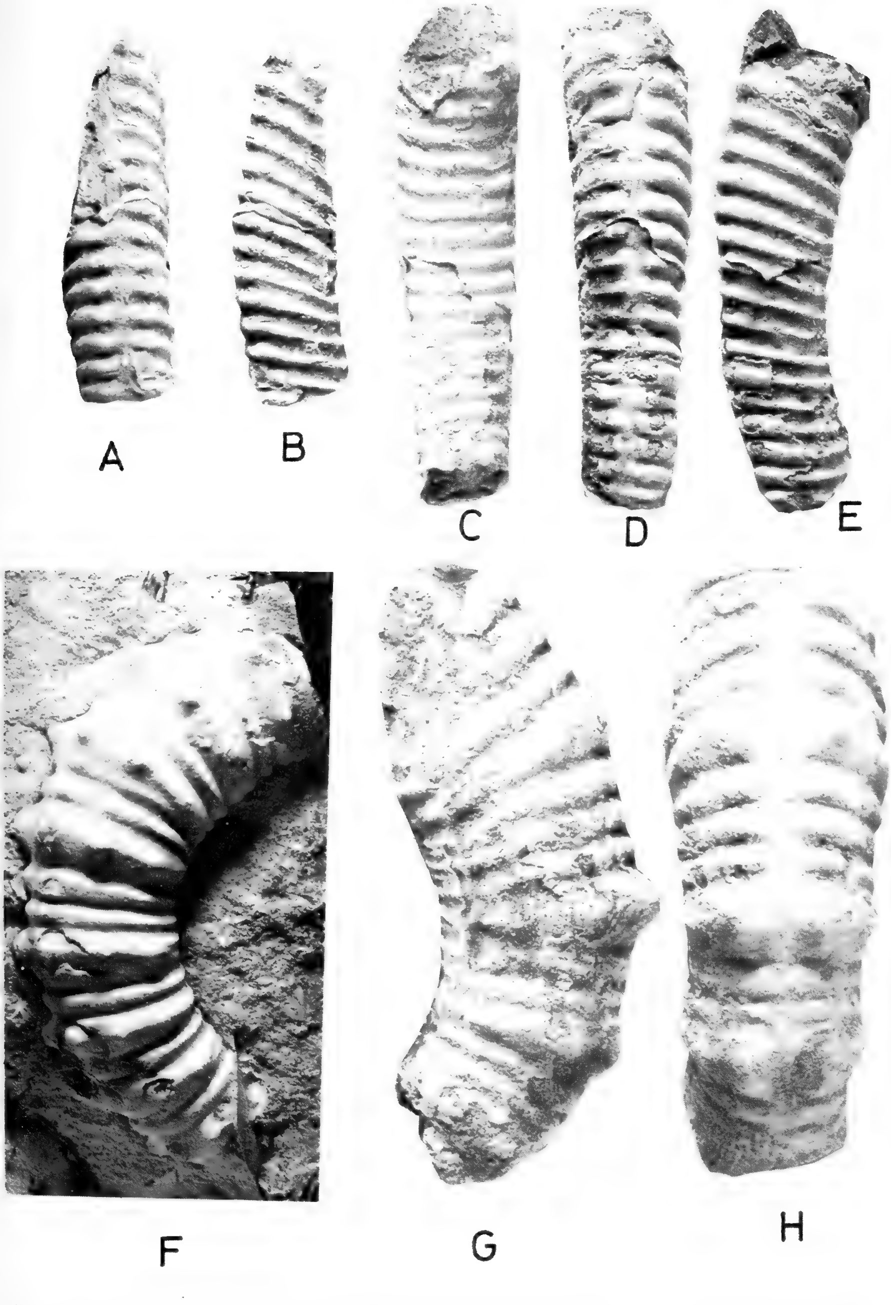


Fig. 68. A–E. *Tonohamites aequicingulatus* (von Koenen, 1902). A–B. BMNH C79692 from locality 166, Zululand, Aptian III. × 2. C–E. BMNH C79690 locality and age as above. × 2. F. *Australiceras* sp. aff. *A. irregulare* (Tenison Woods). BMNH C79714 from locality 167, Zululand, Aptian III–IV. × 1. G–H. *Helicancyloceras* (*Nonyaniceras*) sp. indet. BMNH 79717 from locality 167, Zululand, Aptian III–IV. × 2.

lateral lobe mentioned by Casey (1961: 88) is noticeable in both the Zululand and the Madagascan material.

Occurrence

Tonohamites aequicingulatus occurs in the Lower Aptian *bowerbanki* subzone in England. Von Koenen (1902: 394) referred his specimens to the Aptian and with a question mark to the Zone of *Hoplites deshayesi*. The Madagascan specimen is from the Upper Aptian Zone of *Aconeceras nisus* and *Melchiorites melchioris*.

Tonohamites? caseyi sp. nov.

Fig. 69 (see also Fig. 46)

Holotype

SAS Z804, the specimen marked A from locality 150 or 151, Mkuze Game Reserve. Aptian IV. Geological Survey Collection. Collected by the late Dr E. C. N. van Hoepen.

Derivation of name

Named after Dr R. Casey, Institute of Geological Sciences, London.

Description

Eleven fragments of a heteromorph with labeceratid coiling were partially exposed by preparation from the body chamber of the large *Tropaeum* described above (p. 285).

The holotype shows that coiling is very similar to that of *Tonohamites koeneni* with the early part protruding beyond the venter of the aperture. Ribbing on the early parts is only partially known, and appears to have been strongly rounded and annular. Towards the crozier ribbing becomes more prominent, and the ribs appear to arise at the umbilical edge, are slightly sinusoidal across the flanks, and become progressively wider towards the venter. Over the venter the ribs are broad and elevated, with high-walled interspaces. Occasional bifurcations occur. The suture line is unknown.

Discussion

Initially only part of one specimen was exposed at the venter of the body chamber of the *Tropaeum* sp. After preparation, parts of ten more were found, but due to the hardness of the matrix much of the detail of the specimens has been destroyed.

The labeceratid coiling, and the apparent absence of tuberculation are the most obvious *Tonohamites*-like characteristics. The very striking broad, high-crested ribs on the body chamber are very much like those found in hamitids of the *Hamites gibbosus* type, and point to allocation to *Helicancylus* in the sense of Casey (1961: 85), confirming once more the close relationship between the various helicancylid genera, and the perhaps doubtful validity of retaining *Toxoceratoides*, *Tonohamites* and *Helicancylus* separate.

None of the other Aptian heteromorphs from Zululand has the high-crested crozier ribbing of *T. ? caseyi*; neither has any of the *Tonohamites* or toxoceratoid species described by Casey (1960).

Occurrence

Upper Aptian of Zululand.

Subfamily Heteroceratinae Spath, 1922

Heteromorphs with an initial helix or open spire, followed by planispirally coiled whorls, a curved or straight shaft and recurved crozier are referred to the Heteroceratinae.

Apart from the fact that the group is in need of restudy in the classical European localities, there are some nomenclatorial difficulties, one of which will be discussed below.

A perusal of the literature shows that authorship of the Heteroceratinae (or -dae) is ascribed to either Hyatt 1900 (see Wright 1957: L212; Drushchitz & Kudryavtzev 1960: 296; Dimitrova 1967: 64; Thomel 1964: 62; Vašicec 1972: 57, etc.) or to Spath 1922 (see Luppov & Drushchitz 1958: 105; Egojan 1965: 117; Dimitrova 1970: 94; Kakabadze 1971*a*: 109, 1971*b*: 39, etc.). In the English version of *Zittel's Textbook of Palaeontology* published in 1900, Hyatt, however, never mentioned Heteroceratidae. He included *Hamites* Parkinson, 1811, *Hemibaculites* Hyatt, 1900, *Dirrymoceras* Hyatt, 1900 and *Torneutoceras* Hyatt, 1900, in the Hamitidae, and added 'here should also be placed *Helicoceras* and *Heteroceras* d'Orb., and *Lindigia*, Karstens . . .'. Spath stated (1922: 148) that '*Heteroceras*, *Hemibaculites*, *Dirrymoceras* and *Lindigia* may be united as Heteroceratinae', and from this it should be clear that authorship is referable to Spath (1922) and not to Hyatt (1900).

Some of the most recent comprehensive publications on Heteroceratinae, especially the colchiditids, are by Kotetitchvili (1970) and Kakabadze (1971*a*, 1971*b*).

To the Heteroceratinae may be added *Helicancyloceras* gen. nov. (type species *Heteroceras* (*Argvethites ?*) *vohimaranitraensis* Collignon, 1962) from the Upper Aptian of Madagascar and possibly *Kutatissites* Kakabadze, 1970. The subfamily Heteroceratinae is otherwise represented in the Barremian of Zululand by *Heteroceras* sp. *Colchidites* gr. ex. *colchicus* spp., *Colchidites* sp. indet. and *Paraimerites* sp. These species, and a detailed discussion on the Heteroceratinae are given elsewhere (Klinger 1976).

Helicancyloceras gen. nov.

Type species

Heteroceras (*Argvethites ?*) *vohimaranitraensis* Collignon (1962, pl. 14, pl. 221 (fig. 962), from the Upper Aptian of Madagascar.

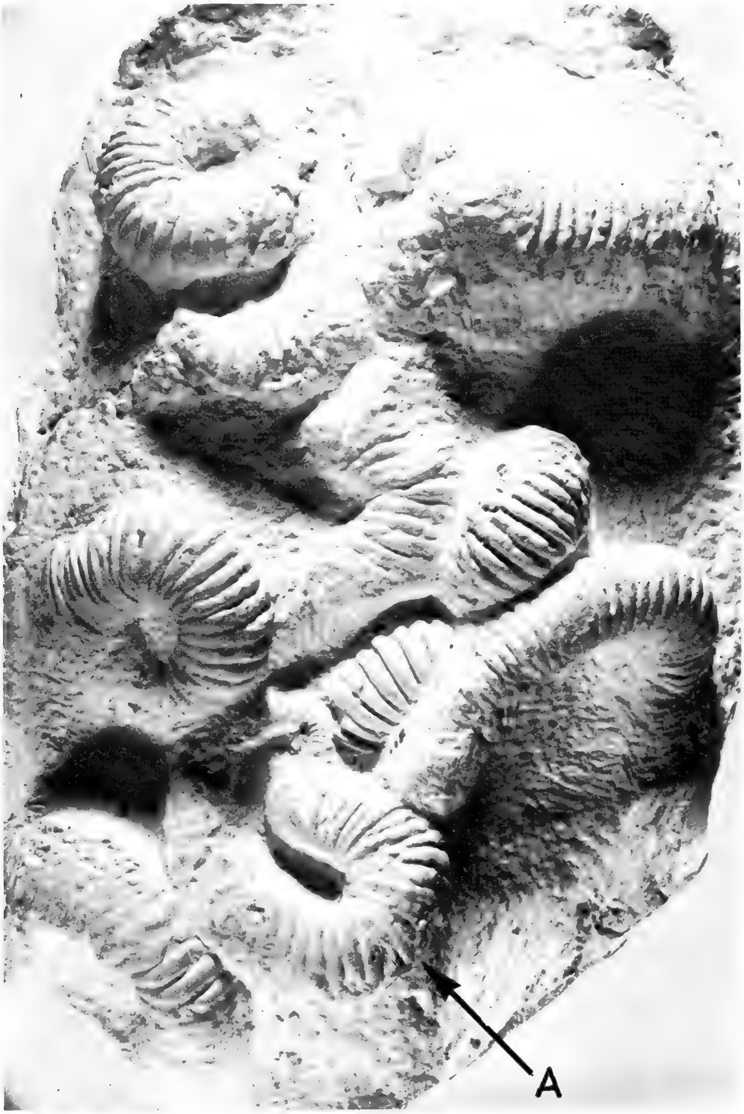


Fig. 69. *Tonohamites? caseyi* sp. nov. SAS Z804 from locality 151, Zululand, Aptian IV. Photograph of cast of original, arrow indicates holotype. × 0,65.

Diagnosis

In typical forms, early whorls coiled in a shallow helix; later whorls may be coiled planispirally in same plane as helix. Size varies considerably, and early species may possibly be more loosely coiled. Ornament consists of ribbing with or without two to three rows of tubercles on each side. Tubercles, if present, become weaker or disappear at varying stages. Lateral, umbilical and internal lobe trifid. Saddles bifid. Age: Upper Aptian.

Helicancyloceras **(*Helicancyloceras*)** subgen. nov.

Diagnosis

Ribbing interrupted over venter in early whorls and ribs may end in small tubercles on either side of the siphonal line. Adult ornament consists of non-tuberculate ribs. Ribs may be flattened over venter with slight forward curvature nearly touching each other, creating 'paternoster' beaded effect.

Helicancyloceras **(*Nonyaniceras*)** subgen. nov.

Type species

Helicancyloceras (*Nonyaniceras*) *nonyani* sp. nov.

Diagnosis

Planispiral coiling is attained rapidly. Early whorls with either ventral or ventral and lateral rows of tubercles on every rib. With increasing diameter intermediary non-tuberculate ribs occur. Tuberculate ribs may be stronger than intermediaries. Umbilical tubercles, if present, very weak. Tuberculation may disappear or become modified at various stages.

Discussion

Abundant fragments of this heteromorph genus occur in the Upper Aptian of Zululand in the Mkuze Game Reserve and along the Mfongozi Creek. Due to the general fragmentary nature of the material, only a few well-defined species may be recognized. The rest of the material is either mentioned or described without specific reference.

The majority of specimens consists of small helices only. Fortunately one specimen (Figs 70–71) shows remains of helical inner whorls, followed by a massive planispiral phragmocone and parts of the body chamber. The authors were at first inclined to regard the helically coiled forms as the ancestors of the larger forms with planispiral outer whorls. Detailed collecting, however, showed that both forms can occur at the same stratigraphic level. Whether the two size groups represent juvenile and adult stages respectively or sexual dimorphs is not known. The predominance of small helices may be due to selective postmortal transport, and may not reflect the true character of the population. In general, however, specimens with well-developed helices dominate at lower stratigraphic levels whereas forms with very shallow helices appear to be younger.

The affinities of the genus are enigmatic. At first glance the helical coils recall the Middle Albian hamitids once referred to d'Orbigny's genus *Helicoceras*. These, however, are true hamitids with a bifid lateral lobe. The helical coiling in *Helicancyloceras* points strongly to the Heteroceratinae, whilst the tuberculate species show ancyloceratine or perhaps helicancyline affinities. As has been pointed out earlier, the subfamilies are primarily accepted because they feature a certain degree of morphological homogeneity. Reference of *Helicancyloceras* to the Heteroceratinae rather than the Ancyloceratinae or Helicancylinae is thus based entirely on morphological criteria.

None of the heteroceratids appears suitable as an ancestral form, mainly because of the time gap between them and *Helicancyloceras*. The heteroceratids with the possible exception of the dubious *Hemibaculites* Hyatt, 1900, are restricted to the Barremian. Nevertheless, the relationship of *H.* (*Helicancyloceras*) to *H.* (*Nonyaniceras*) is similar to that of *H.* (*Heteroceras*) to *H.* (*Argvethites*) or of *Colchidites* to *Imerites*.

The very enigmatic genus *Kutatissites* Kakabadze, 1970 (type species *K. bifurcatus* Kakabadze, 1970), thus far known only from the Late Barremian of Georgia (U.S.S.R.) and France is another helically coiled form which may be considered ancestral. Thieuloy (1976) provides an extensive description of the French representative of this species, *K. edwardsi* (Reynes, 1876) and tentatively refers the genus to the Helicancylinae. Again the difference in age (late Barremian vs late Aptian) seems to stand in the way of deriving *Helicancyloceras* directly from *Kutatissites*.

Representatives of the Ancyloceratinae may provide the answer. *Helicancyloceras* could possibly be derived from an australiceratid such as *Australiceras irregulare* (Tenison Woods) with irregular early whorls not lying in one plane (see Day 1974, pl. 2 (Fig. 3)). *Australiceras* loses tuberculation in the middle stages of life. In the hypothetical ancestor of *Helicancyloceras* (*Helicancyloceras*), reduction of tuberculation could have affected the early whorls already, whereas the reduction in *H.* (*Nonyaniceras*) could have been retarded. In this case the relationship of *H.* (*Helicancyloceras*) to *H.* (*Nonyaniceras*) would be somewhat analogous to that of *Tropaeum* to *Australiceras* as far as the presence or absence of tubercles is concerned.

Whatever the origin of *Helicancyloceras* may be, the ornamentation and mode of coiling combines features of Ancyloceratinae, Helicancylinae and Heteroceratinae, again pointing to the rather artificial status of these groups. Reference of *Helicancyloceras* to the Heteroceratinae is done for pure morphological reasons, in full cognizance that this might imply a diphyletic origin for the Heteroceratinae (if they are to be retained as a separate group).

Furthermore, *Helicancyloceras* illustrates another attempt towards recoiling, and thus, (presumably) a more active mode of life for the animals concerned.

Helicancyloceras (*Helicancyloceras*) *vohimaranitraensis* (Collignon, 1962)

Figs 70, 71A–B, 73B, D, 74A–F, 75B–C, E–G, 76A–B?, 77D–E, ?F–G, 78C, 88A–C

Heteroceras (*Argvethites?*) *vohimaranitraensis* Collignon 1962: 14, pl. 221 (fig. 962). Klinger 1976: 14, pl. 1 (nos. 3–5), figs 5d–e, 6b–e.

Holotype

Collignon's (1962, pl. 221 (fig. 962)) specimen from the Upper Aptian of Betioky, Madagascar.

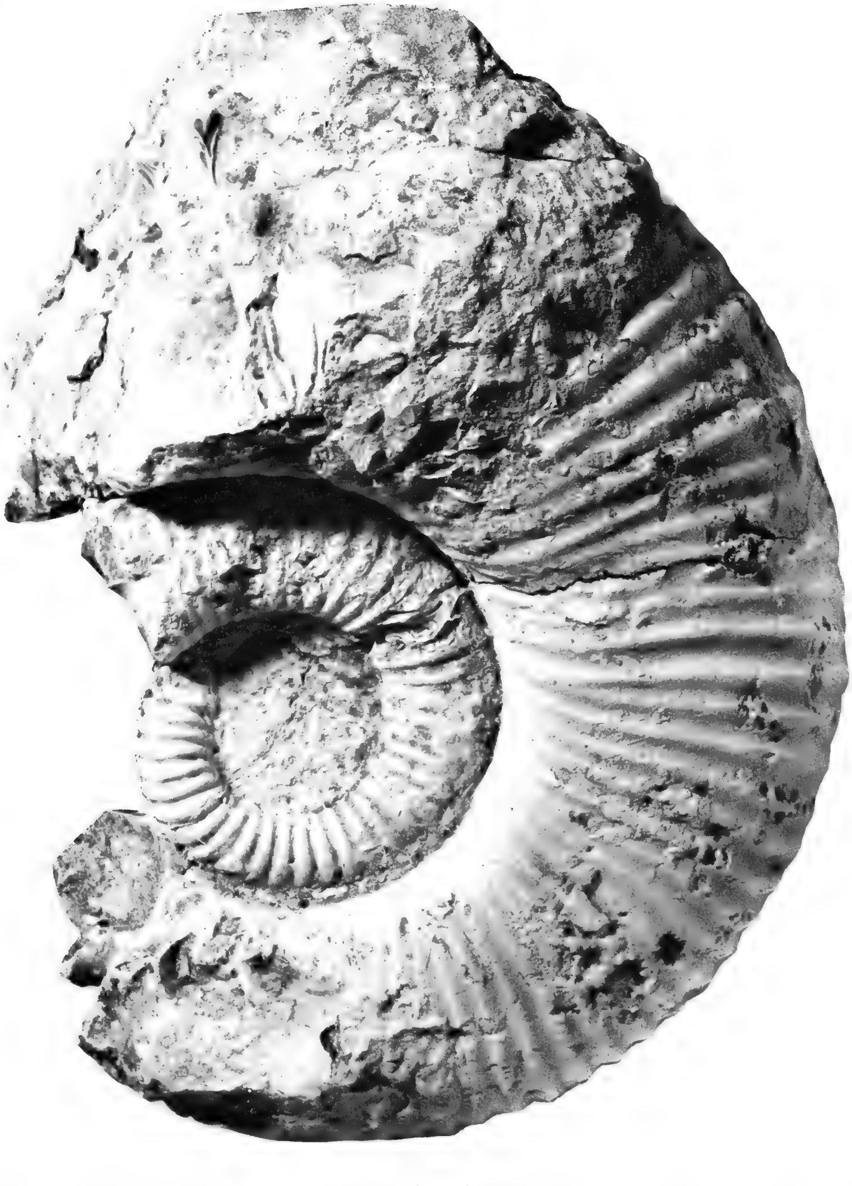


Fig. 70. *Helicancyloceras* (*Helicancyloceras*) *vohimaranitraensis* (Collignon, 1962). SAS H71D from locality 152, Mkuze Game Reserve, Zululand, Aptian IV. Largest available specimen with helicoid inner whorl, but completely symmetrical planispirally-coiled outer whorl. × 0,86. (See also Fig. 71.) Possible sexual dimorph?

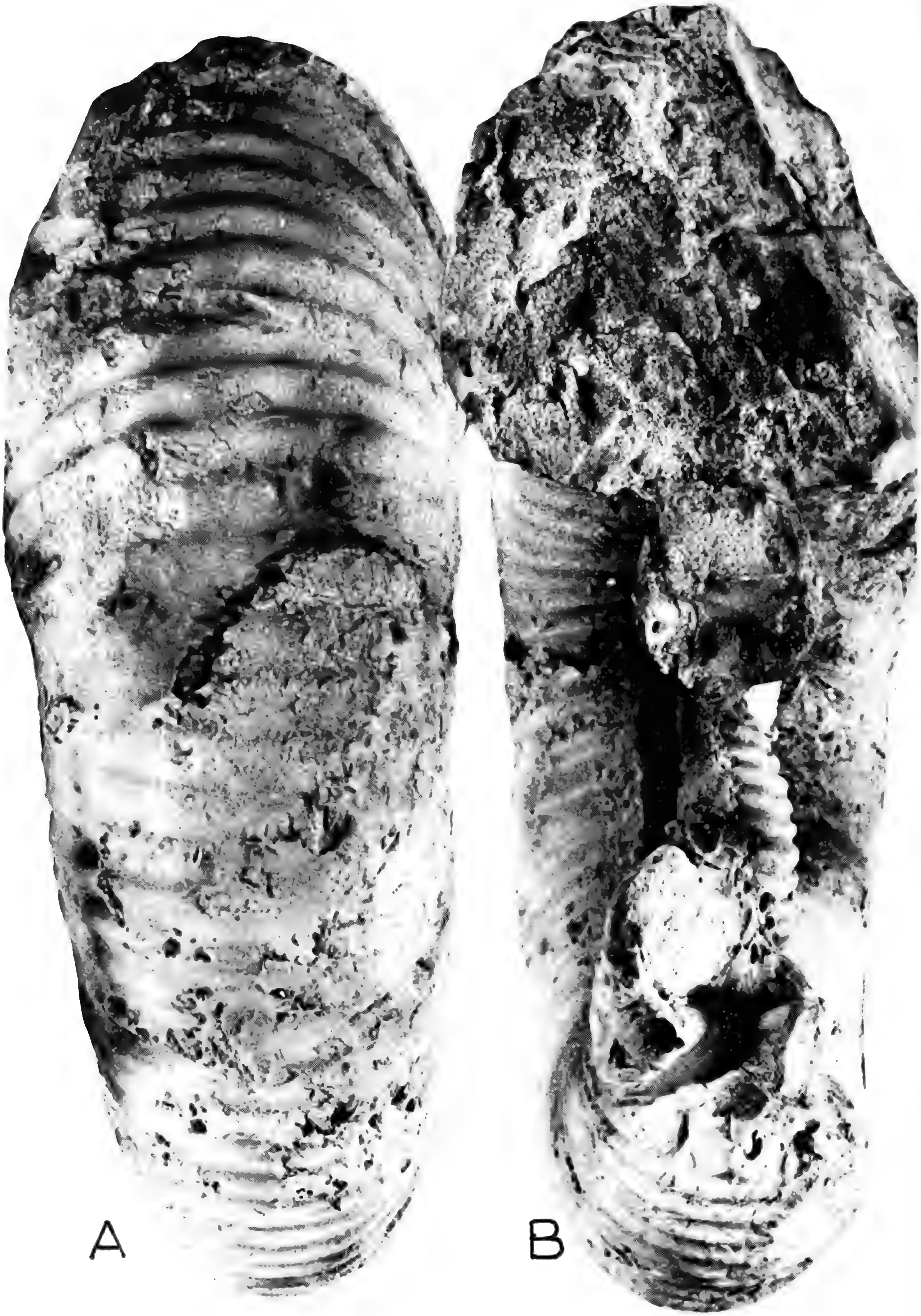


Fig. 71. A–B. *Helicancyloceras* (*Helicancyloceras*) *vohimaranitraensis* (Collignon, 1962). SAS H71D from locality 152, Mkuze Game Reserve, Zululand, Aptian IV. Note the helical inner whorl. × 0,75.

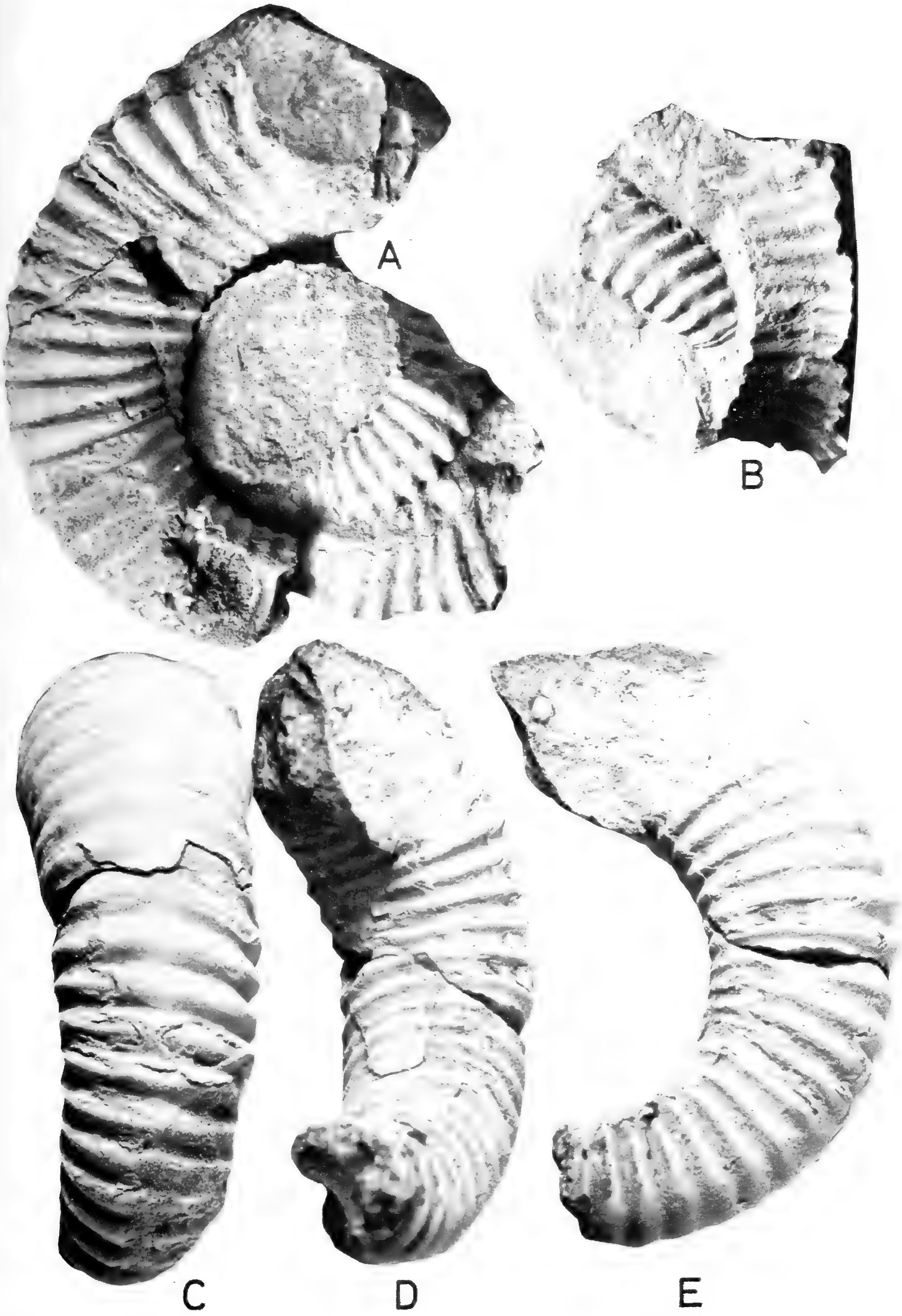


Fig. 72. A–E. *Helicancyloceras* (*Nonyaniceras*) *circulare* sp. nov. BMNH C79718 from locality 166, Zululand, Aptian III. × 2.

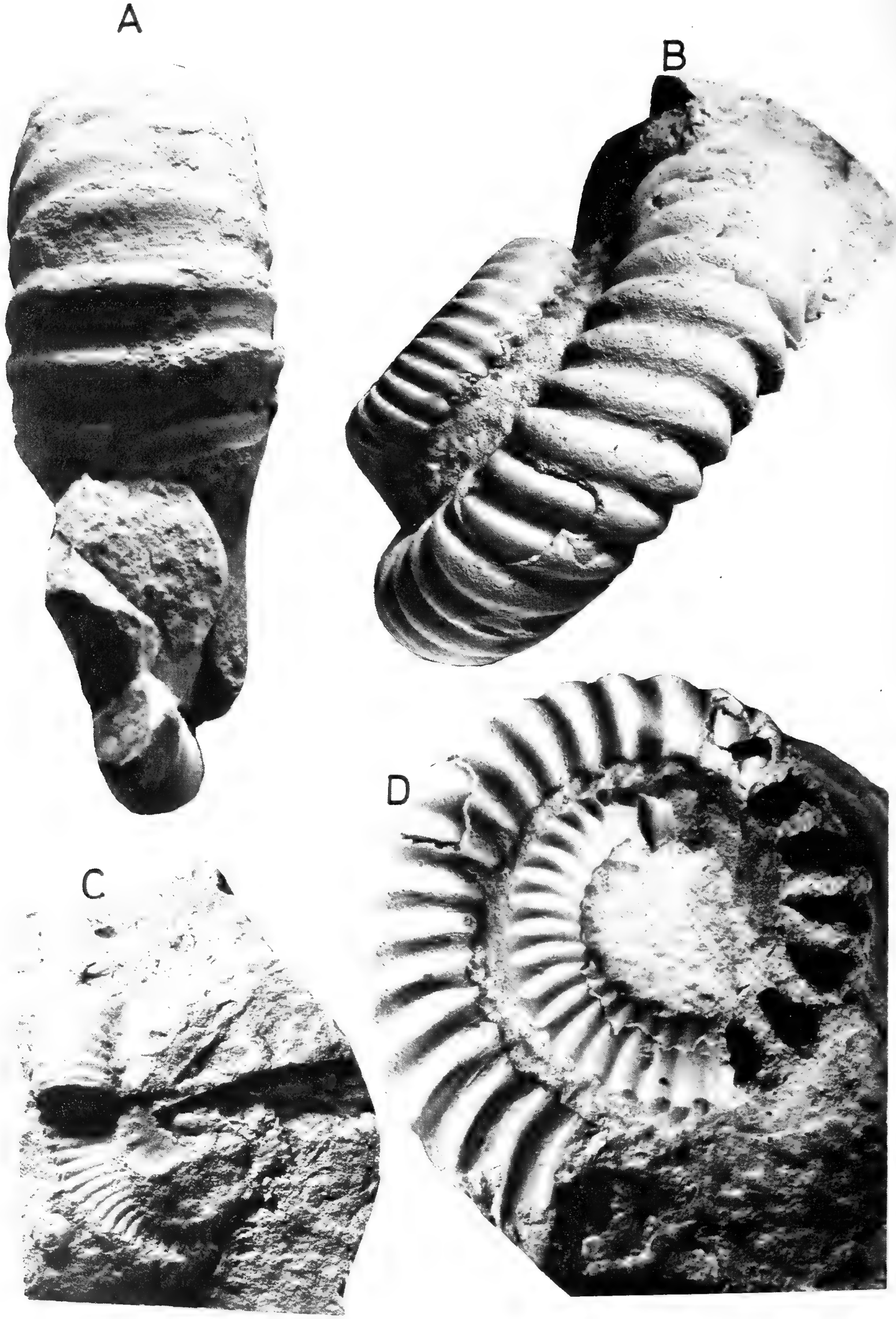


Fig. 73. A. *Tonohamites koeneni* Casey, 1961. SAS Z1115 from locality 152, Zululand, Aptian IV. × 1,3. B, D. *Helicancyloceras* (*Helicancyloceras*) *vohimaranitarensis* (Collignon, 1962). SAS Z9(5) from locality 168, Zululand, Aptian III–IV. This is an extremely coarsely ribbed specimen. × 1,6. C. *Helicancyloceras* (*Helicancyloceras*) sp. indet. × 1,5.

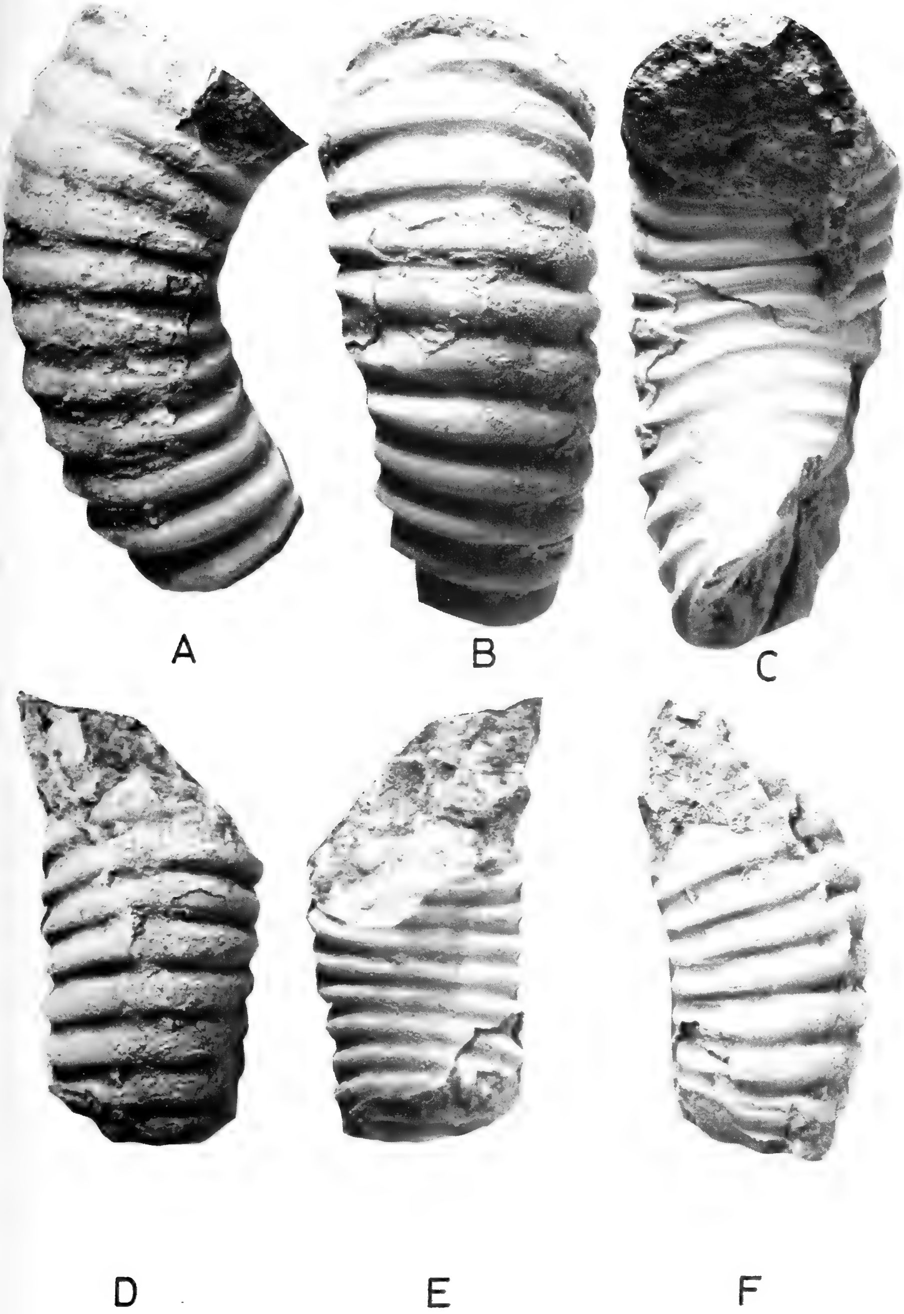


Fig. 74. A–F. *Helicancyloceras* (*Helicancyloceras*) *vohimaranitraensis* (Collignon, 1962). A–C. BMNH C74709 from locality 166, Zululand, Aptian III. × 2. D–F. BMNH C79711, same locality and age as above. × 2.

Material

SAS Z8(6), SAS Z8/3, SAS 871D/12, SAS H71D, SAS Z1153, all from locality 168 and 152. Aptian III–IV: BMNH C79703–C79712, all from locality 166, Aptian III.

Description

Early stages of growth are helical, either dextral or sinistral, consisting of about one and a half to two whorls. The distance between the successive whorls is extremely variable. After the helical stage coiling becomes planispiral in some specimens.

Ornament in the helix consists of prominent ribs, narrowest and least prominent on the dorsum, wedge-shaped on the flanks and broadest over the venter. Interspaces on the flanks are about as wide as the ribs. Ribbing over the venter is very variable. At small diameters the ribs are interrupted or weakened on the venter, in some cases forming small pimple-like tubercles on either side of the siphonal line. At large diameters the ribs cross the venter with a slight forward curvature and a thickening in the interspaces, thus forming a 'paternoster' effect. In the planispiral part of the shell the ribbing becomes finer and wider-spaced and somewhat rursiradiate. Ribbing over the dorsum is very weak at this stage. Occasional bifurcations occur at the umbilical edge. On the body chamber the whorl section becomes dome-shaped with a flattened dorsum and broadly inflated flanks and venter. The suture line is relatively simple with bifid saddles and trifid L, U, I lobes. L is largest and U smallest.

Dimensions

Specimen	*D*	*Wb*	*Wh*	*Wb/Wh*	*U*	*H* (height of spire)
H71D	175	64(36,7)	76(44,7)	0,84	64(36,5)	—
SAS Z9(5)	46	14(30,4)	12(26)	1,17	22(47,8)	23

Discussion

As can be seen from the figures, the species is interpreted rather widely, and is intimately connected to *H.* (*H*) *densecostatum* sp. nov. by finer-ribbed specimens such as BMNH C79713 (Fig. 75B–C), SAS Z8/Hd (Fig. 76B) and SAS A1294 (Fig. 79C). It is similarly connected to *H.* (*N.*) *circulare* from which it differs in becoming planispiral at later stages and in lacking regular tuberculation in the early stages of growth.

The occurrence of both large and small forms at the same stratigraphic level (e.g. SAS H71D and SAS H71D/12, Figs 70, 71A–B, 76A) is of interest; sexual dimorphism seems the most likely explanation. The helical inner whorls of the large specimen SAS H71D are indistinguishable from isolated helices or fragments of helices, indicating conspecificity, and, that in some cases at least, the shell changes to a planispiral mode of coiling after an initial helical stage.

The inner whorls are easily distinguished from other heteromorphs occurring at this stratigraphic level by the helical coiling and curious mode of ornament over the venter. Small fragments bear similarity to the inner whorls of *Tropaeum*, but are distinguished by the oblique ribbing. Small pieces of *Tonohamites koeneni*, which occur at the same level, are distinguished by the same character.

The outer, planispiral whorls, with symmetrical ribbing are easily mistaken for *Tropaeum* or *Australiceras*, and, unless associated with the inner whorls, may be indistinguishable.

Occurrence

The species occurs in the Upper Aptian zone of *Epicheloniceras tschernischewi* of Madagascar, and Aptian III–IV of Zululand.

Helicancyloceras* (*Helicancyloceras*) *densecostatum sp. nov.

Figs 67A–B, 75B–C?, I–J, 76B?, 79C, 81D

Heteroceras (*Argvethites?*) *vohimaranitraensis* Klinger, 1976: 14 (pars), pl. 2 (no. 5) only.

Holotype

SAM–PCZ5682 from locality 168 Mfongozi Creek, Zululand. Aptian III–IV. South African Museum Collection. Collected by H. Klinger.

Material

Apart from the holotype, SAS LJE138, SAS A294, A1294, SAS Z8/6 from locality 168 and BMNH C79713 from locality 166 Mfongozi Creek, Zululand. Aptian III–IV.

Description

The initial helix is very low and consists of about one whorl. Coiling becomes planispiral at an early stage. The whorl section is rounded throughout.

Ornament consists of very fine ribs, approximately twenty-five per half whorl, separated by interspaces of comparable width. On the earliest whorls preserved, the ribbing is distinctly interrupted over the venter, each rib ending in a minute tubercle on either side of the siphonal line. With increasing diameter, the ventral interruption of ribbing disappears and is present as a mere swelling on each rib along the siphonal line, again creating a 'paternoster' effect. On specimen SAS A1294 (Fig. 79C) ventral tubercles occur on the body chamber on two ribs, separated by five intermediaries.

Dimensions

Specimen	*D*	*Wb*	*Wh*	*Wb/Wh*	*U*	*H*
SAM PCZ5682	42	18(42,8)	16(38,1)	1,12	23(50)	14

Discussion

The diagnostic characteristics of the species are the fine ribbing and the very shallow helix. Whereas *H.* (*H*) *vohimaranitraensis* has about 15 ribs per

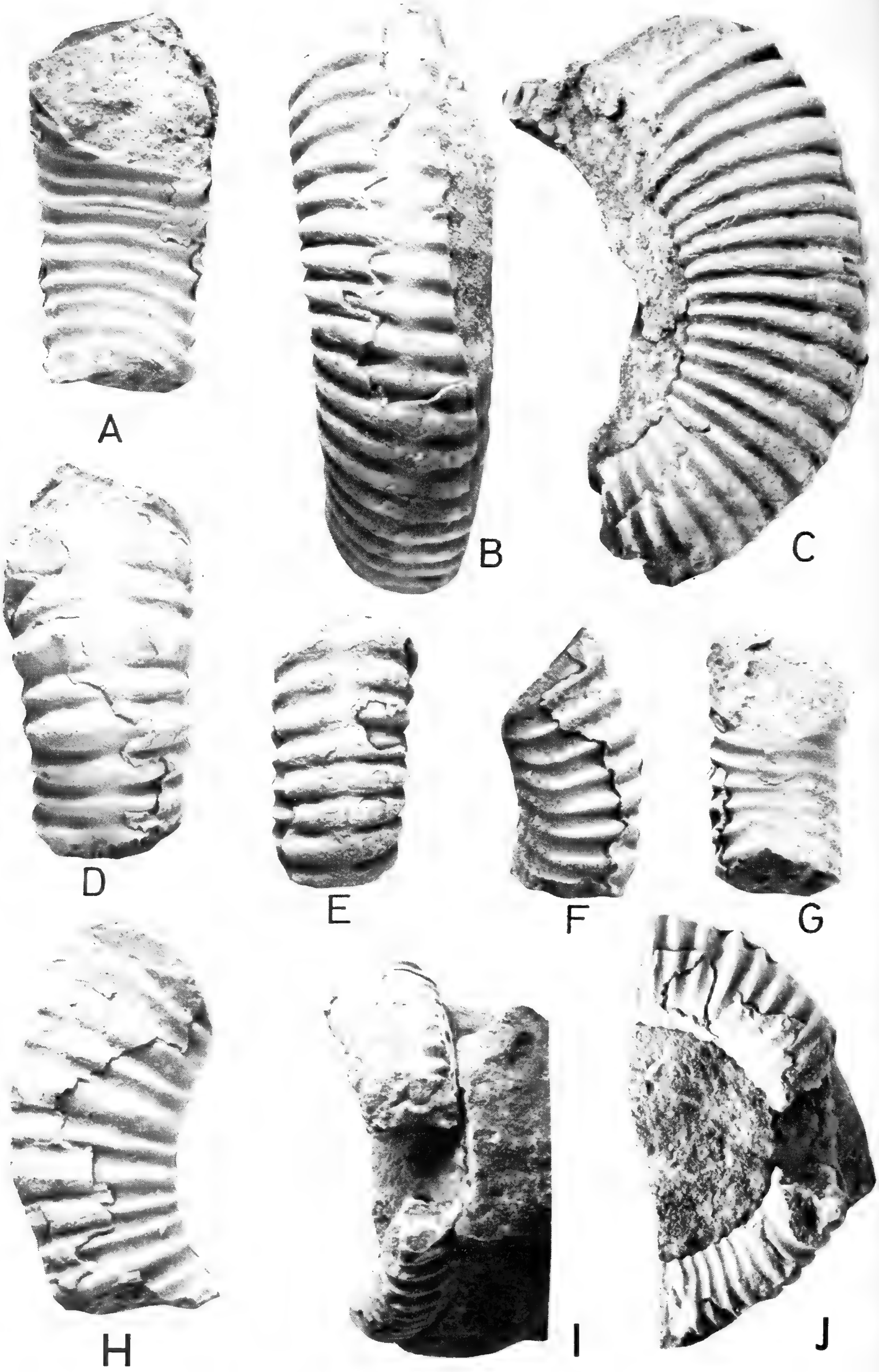


Fig. 75. A, D, H. *Helicancyloceras* (*Nonyaniceras*) sp. indet. BMNH C79698 from locality 166, Zululand, Aptian III. × 2. B–C. *Helicancyloceras* (*Helicancyloceras*) *vohimaranitraensis* (Collignon, 1962). BMNH C79704 from locality 166, Zululand, Aptian III. × 2. Transitional to *H.* (*H.*) *densecostatum*. E–G. *Helicancyloceras* (*Helicancyloceras*) *vohimaranitraensis* (Collignon, 1962). BMNH C79705 from locality 166, Zululand, Aptian III. I–J. *Helicancyloceras* (*Helicancylo ceras*) *densecostatum* sp. nov. BMNH C79706 from locality 166, Zululand, Aptian III. × 2.

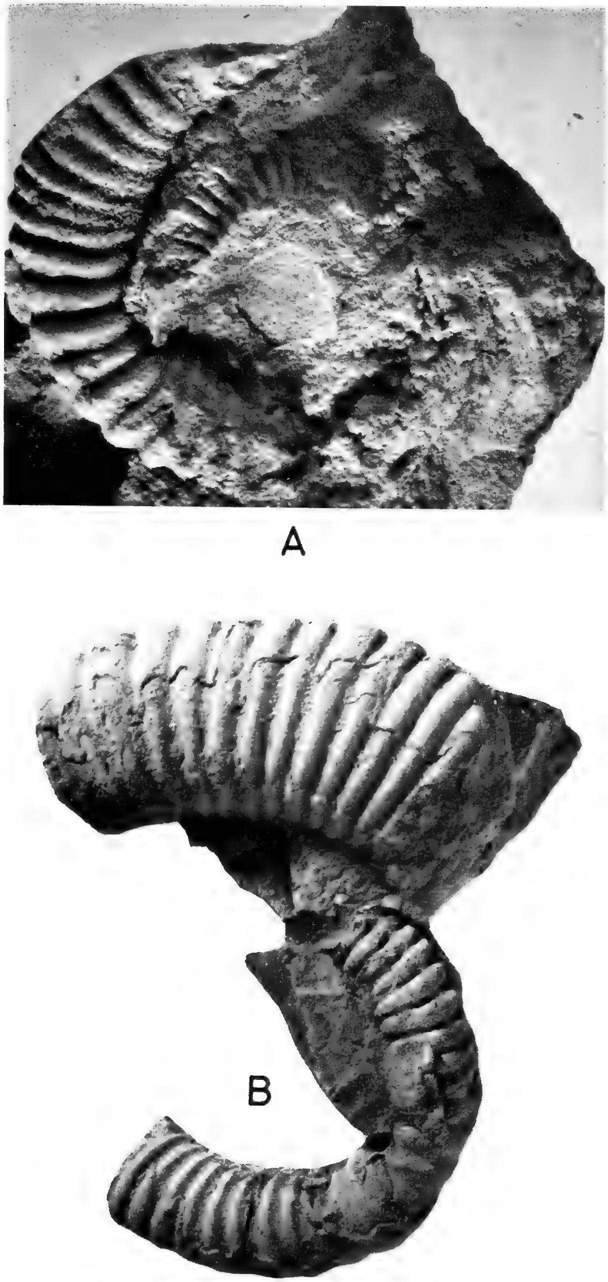


Fig. 76. *Helicancyloceras* (*Helicancyloceras*) *vohimaranitraensis* (Collignon, 1962). A. SAS H71D/12 from locality 152, Zululand, Aptian IV. × 1,8. B. SAS Z8/Hd × 1,5 from locality 168, Aptian III–IV. Transitional to *H.* (*H.*) *densecostatum* sp. nov. × 1,7.

Fig. 77. A–C. *Helicancyloceras* (*Nonyaniceras*) *circulare* sp. nov. BMNH C79708 from locality 166, Zululand, Aptian III. × 2. D–E. *Helicancyloceras* (*Helicancyloceras*) *vohimaranitraensis* (Collignon, 1962). BMNH C79710 from locality 166, Zululand, Aptian III. × 2. F–G. *Helicancyloceras* (*Helicancyloceras*) sp. indet. BMNH C79693 from locality 166, Zululand, Aptian III. × 2.

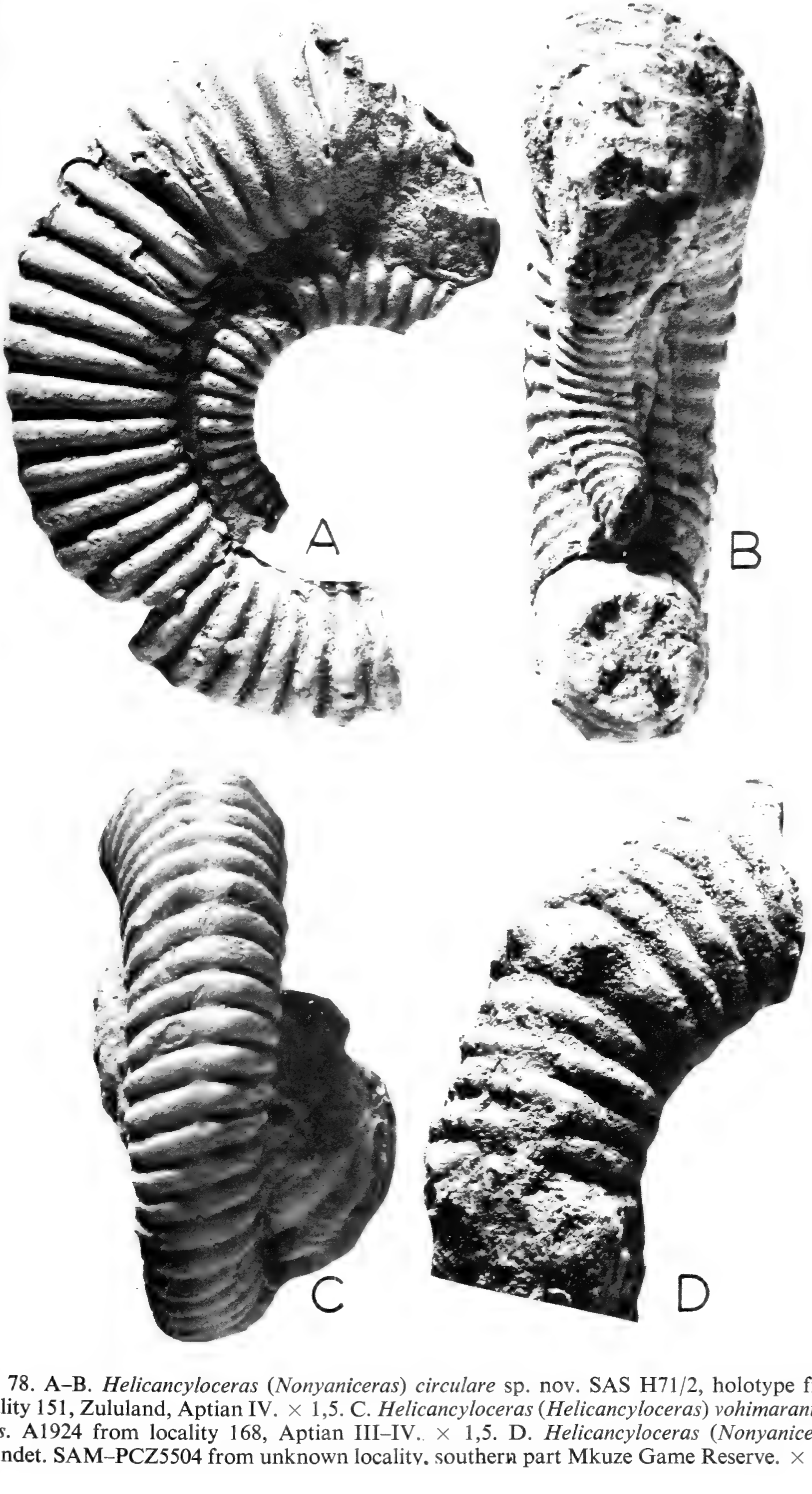


Fig. 78. A–B. *Helicancyloceras* (*Nonyaniceras*) *circulare* sp. nov. SAS H71/2, holotype from locality 151, Zululand, Aptian IV. × 1,5. C. *Helicancyloceras* (*Helicancyloceras*) *vohimaranitraensis*. A1924 from locality 168, Aptian III–IV. × 1,5. D. *Helicancyloceras* (*Nonyaniceras*) sp. indet. SAM–PCZ5504 from unknown locality, southern part Mkuze Game Reserve. × 1,5.

half whorl, *H.* (*H*) *densecostatum* has about 25. Transitional forms like SAS Z8/Hd (Fig. 76B) with 21 ribs per half whorl connect the species and may be referred to either. The presence of tubercles on the body chamber of some specimens points to affinities with *H.* (*Nonyaniceras*). The presence of tubercles in the very early and late stages with a non-tuberculate middle stage is a situation comparable to that found in *Australiceras*. It is not known if large forms also occur in this species, but the outer whorl is virtually bilateral symmetrical.

Occurrence

Upper Aptian of Zululand.

Helicancyloceras (*Helicancyloceras*) spp. indet.

Several small fragments of heteromorphs with *Helicancyloceras*-like ornament are too poorly preserved for specific identification. A specimen in the collection of the Geological Survey, Z8/21, here figured as Figure 81E is a slightly twisted fragment with the typical ornament over the venter, but does not appear to have been helically coiled. BMNH C79693 is also only slightly curved, indicating looser coiling in, as yet, unknown species of the genus.

Helicancyloceras* (*Nonyaniceras*) *nonyani sp. nov.

Figs 82A–B, 83B

Holotype

SAS LJE182 from locality 168, Mfongozi Creek, Zululand. Aptian III–IV. Geological Survey Collection. Collected by L. J. Engelbrecht.

Derivation of name

The species is named for Mr Johannes Nonyane, Klinger's field assistant and laboratory preparator from 1967 to 1975.

Material

Only the holotype.

Description

The early whorl forms a very shallow helix, and on the second, and last whorl, coiling is perfectly bilaterally symmetrical at the aperture. The body chamber occupies slightly less than one half of a whorl of the holotype.

The whorl section on the early whorl is round, but becomes ovoid, higher than wide in the body chamber. Initial ornament consists of narrow, rounded radial ribs, separated by interspaces of similar width, each bearing a pair of ventral tubercles. At a diameter of approximately 8 mm, ornament becomes irregular, lateral tubercles appear and the ribs develop a prorsiradiate curvature. On the body chamber the ribs pass over the dorsum with a slight forward curvature, but much weakened. The ribs are narrowest at the umbilical edge, becoming broader towards the venter. Five ribs on the body chamber have prominent ventral tubercles, separated by one to three intermediaries. Lateral tubercles situated on the ventral third of the flanks are developed only on one side, due to injury. Ventral tubercles are variably developed on the intermediaries. They may appear as distinct tubercles or merely as slight edges on the ventrolateral sides of the whorl. The major ribs are slightly thickened and flattened between the lateral and ventral tubercles, and also over the venter, forming incipient loops. Slight thickenings occur between the ribs along the siphonal line, creating a 'paternoster' effect.

Discussion

The distinct ventral tuberculation and prominent ribbing on the body chamber clearly separates this species from other *Helicancyloceras* and deserves subgeneric rank. The angular costal whorl section on the body chamber is superficially similar to that of *Pedioceras cundinamarcaea* Karsten, 1886, from the Barremian of Colombia (see Wright, 1957: L202, fig. 237: 5a–c). That however, is as far as the similarity goes. *Pedioceras cundinamarcaea* has a distinct dorsal zone of impression and is coiled planispirally.

Occurrence

Upper Aptian, Aptian III–IV of Zululand.

Helicancyloceras* (*Nonyaniceras*) *circulare sp. nov.

Figs 72A–E, 77A–C, 78A–B

Holotype

SAS H71/2 from locality 151, Mkuze Game Reserve. Aptian IV. Geological Survey Collection. Collected by H. C. Klinger.

Material

The holotype and BMNH C79698, BMNH C79708, BMNH 79718 from locality 166, Aptian III.

Description

The initial helix is very shallow as can be seen in Figure 77A–C, and bilateral symmetry is attained rapidly. The whorl section is circular. Ornament on the inner whorl consists of fine, slightly prorsiradiate ribs, each bearing weak ventral and lateral tubercles. On the outer whorl the ribs are stronger, prominently rounded and separated by narrow interspaces. Two quadrituberculate ribs, separated by three non-tuberculate ribs, are present at the smaller end of the outer whorl of the holotype. The tubercles, lateral and ventral, are very small and pointed.

Discussion

The presence of the two rows of tubercles on all ribs of the inner whorl, and the strong, rounded ribbing on the outer whorl, combines features of both subgenera, showing the close relationship between the two. The outer whorl might easily be mistaken for a juvenile *Tropaeum*, as coiling is already planispiral and, unless accompanied by the inner whorls, distinction from *Tropaeum* would be difficult. The very low helix plus the presence of tubercles on the inner whorls and at larger diameters serves to distinguish the species from *H.* (*H.*) *vohimaranitraensis*.

Occurrence

Upper Aptian of Zululand, Aptian IV.

Helicancyloceras* (*Nonyaniceras*) *crassetuberculatum sp. nov.

Fig. 79E–F

Holotype

SAS L65/13 from locality 168, Mfongozi Creek, Zululand. Aptian III–IV. Geological Survey Collection. Collected by H. Klinger, 1970.

Material

Apart from the holotype, SAS L65/14 from the same locality.

Description

The holotype consists of half a whorl. The whorl section is rounded. The original helix must have been very shallow, but the helical coiling is nevertheless rendered distinct by the asymmetry of ornament over the venter. Ornament consists of major trituberculate ribs, separated by one to three narrower intermediaries. The umbilical tubercles are smallest, and virtually absent at the smallest diameters visible. The ventrolateral and ventral tubercles are conical, very prominent, and situated close together. On the flanks the trituberculate ribs show signs of flattening or duplication. Ribbing is weakened on the dorsum, and the major ribs duplicate at larger diameters. The intermediary ribs are weakly tuberculate over the venter at small diameters. With increasing diameter the tuberculation becomes less noticeable.

Discussion

H. (*N.*) *crassetuberculatum* is distinguished from other species of the subgenus by the very prominent tuberculation at small diameters. Fragments bear similarity to *Ancyloceras*, but the asymmetry of ornament over the venter reveals the generic affinity.

Anderson's *Helicancylus gabbi* (1938: 222, pl. 79 (figs 4–5)) is a similar helical form of uncertain generic affinity. The ribbing, however, is much stronger and there are fewer intercalatories. As yet the systematic position of

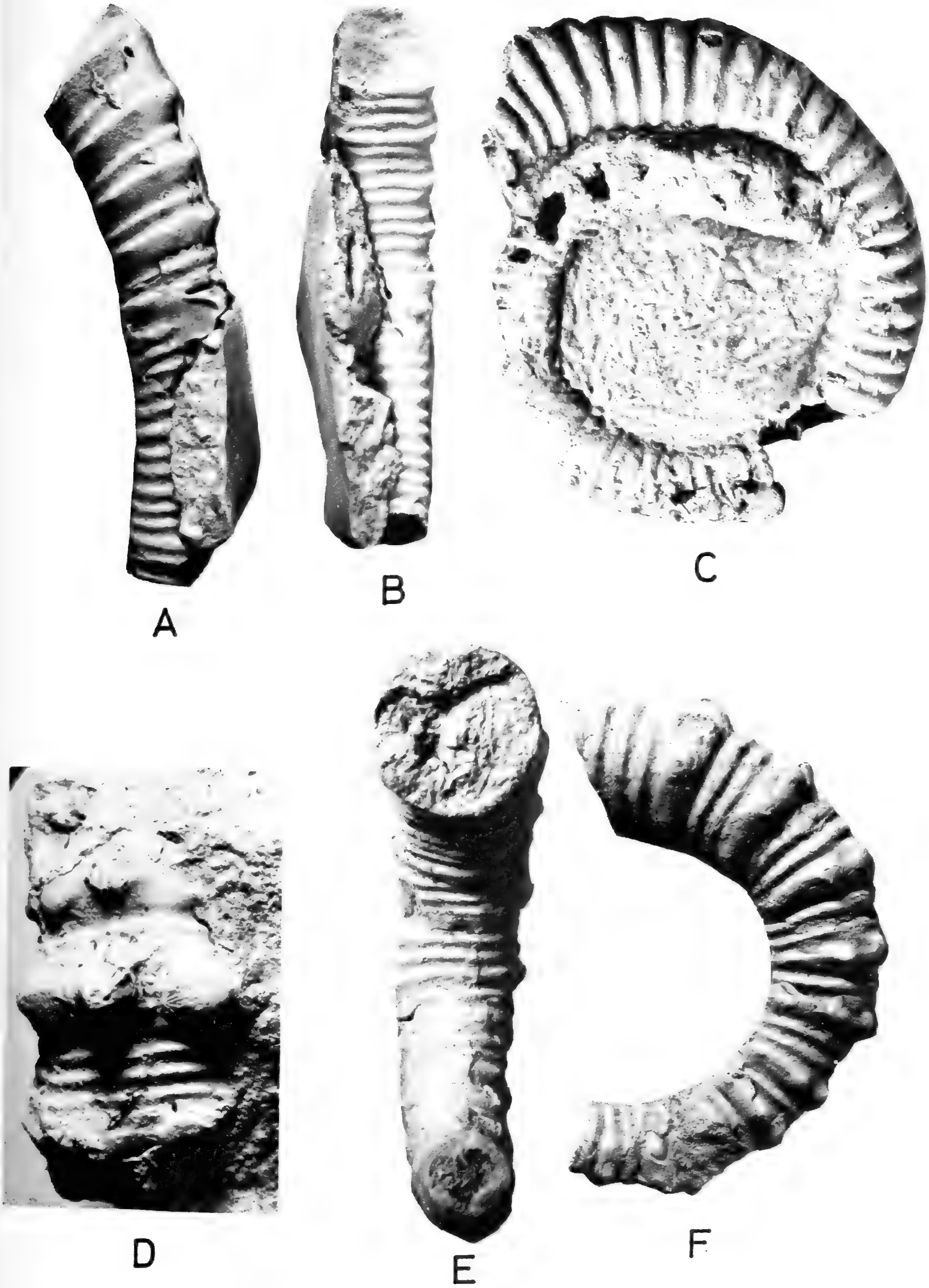


Fig. 79. A–B. *Toxoceratoides? haughtoni* sp. nov. SAS Z8/Ti from locality 168, Zululand, Aptian III–IV. × 1,6. C. *Helicancyloceras* (*Helicancyloceras*) *densecostatum* sp. nov. SAS A1294 from locality 168, Zululand, Aptian III–IV. × 1,55. D. *Ancyloceras* (*Ancyloceras?*) sp. indet. SAS H54/39 from locality 170, Zululand, Aptian I. × 1,5. E–F. *Helicancyloceras* (*Nonyaniceras*) *crassetuberculatum* sp. nov. SAS L65/13, holotype from locality 168, Zululand, Aptian III–IV. × 1,5.

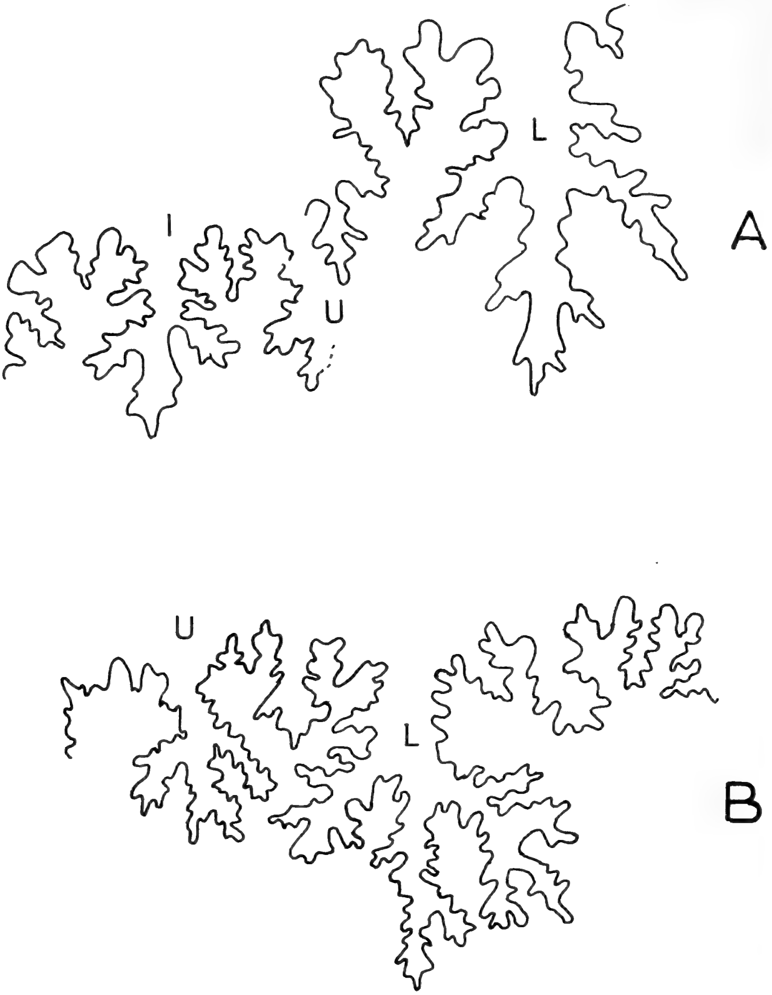


Fig. 80. A. Suture line of *Australiceras* sp. aff. *irregulare* (Tenison Woods, 1883). SAM–PCZ5506. × 3. B. Suture line of Z8n, Insertae sedis. × 1.

this species is not known, and it is not certain if the specimen is congeneric with the hamulinid *Helicancylus aequicostatus* (Gabb).

Ancyloceras helicoides Rouchadzé (1933: 17, pl. 8 (fig. 3) is another ancyloceratid form, but again the tuberculation is much stronger and is referred to *Kutatissites* of Late Barremian age.

Occurrence

Upper Aptian of Zululand.

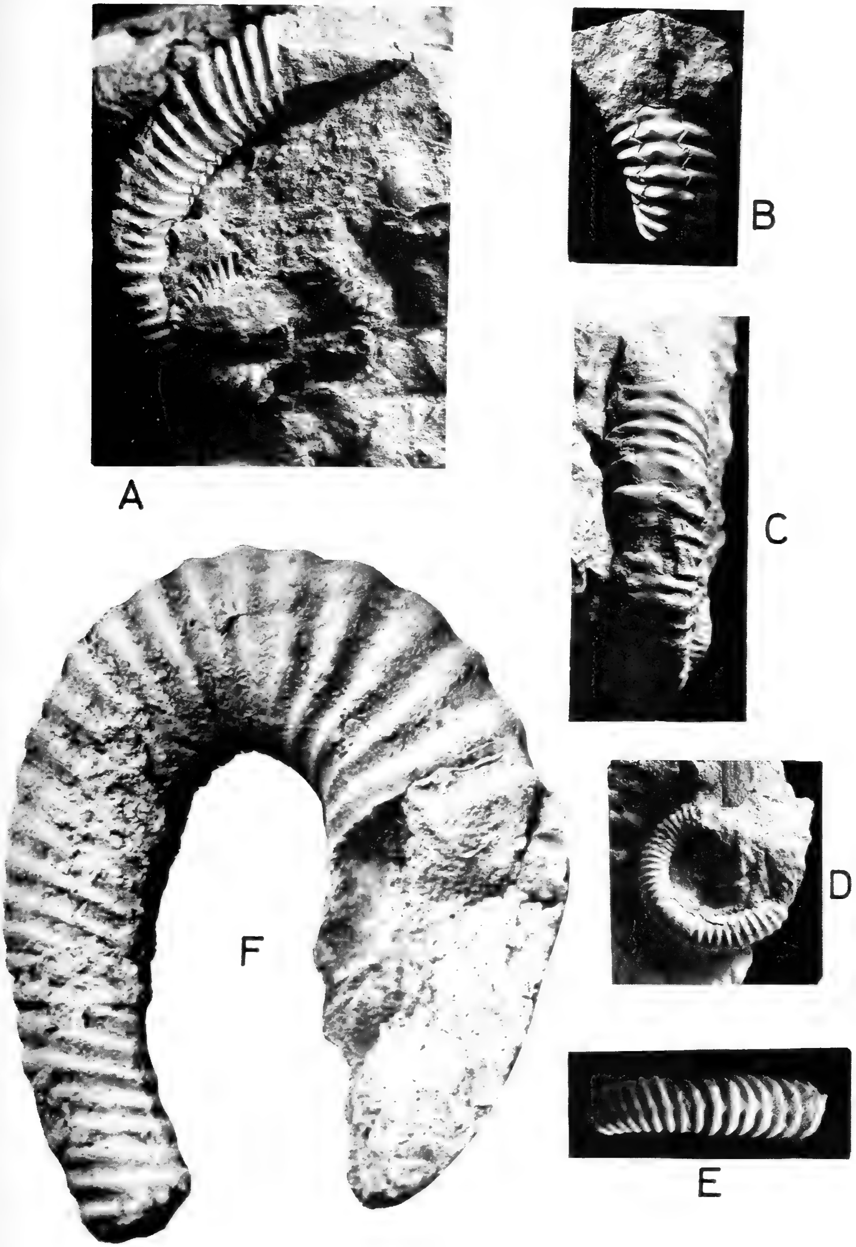


Fig. 81. A, C. *Helicancyloceras* (*Nonyaniceras*) sp. indet. SAS Z8(7) from locality 168, Aptian III–IV. × 1. B. *Helicancyloceras* (*Nonyaniceras*) sp. indet. SAS H71D/15 from locality 152, Zululand, Aptian IV. × 1. D. *Helicancyloceras* (*Helicancyloceras*) *densecostatum* sp. nov. SAS LJE 138 from locality 168, Zululand, Aptian III–IV. × 1. E. *Helicancyloceras* (*Helicancyloceras*) sp. indet. Unnumbered specimen SAS collection. × 1. F. *Tonohamites koeneni* Casey, 1961. SAS Z193 from locality 152, Zululand, Aptian IV. × 1,5.

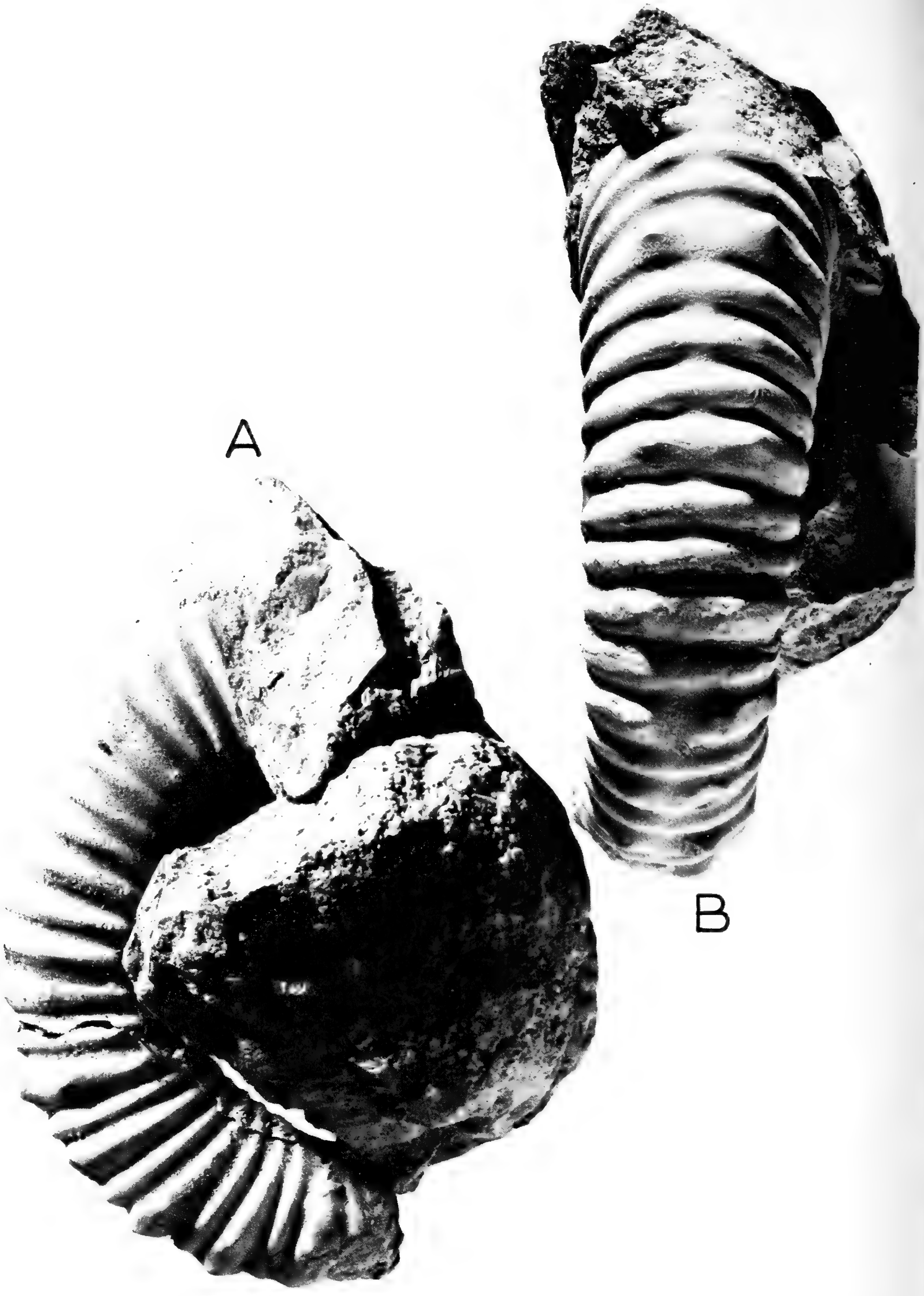


Fig. 82. A–B. *Helicancyloceras* (*Nonyaniceras*) *nonyani* sp. nov. SAS LJE182, holotype from locality 168, Zululand, Aptian III–IV. × 1,6 (See also Fig. 83B.)

Fig. 83. A. *Lithancylus* sp. SAM–PCM5436 from Lubemba, Mozambique, Lower Aptian. Dorsal view. × 1,2. B. *Helicancyloceras* (*Nonyaniceras*) *nonyani* sp. nov. SAS LJE182, holotype from locality 168, Zululand, Aptian III–IV. Tuberculation absent on body chamber due to pathological disturbance. × 1. C–D. *Helicancyloceras* (*Nonyaniceras*) sp. indet. SAM–PCZ5504 from unknown locality in southern part of Mkuze Game Reserve. × 1,3.

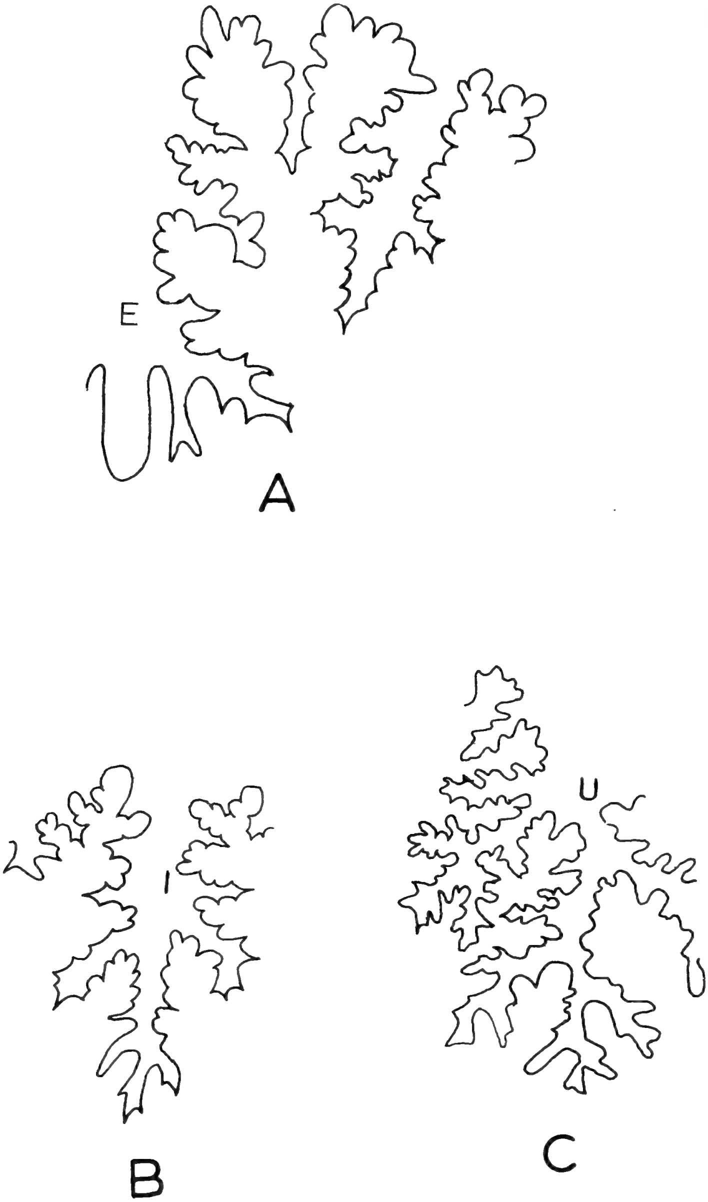


Fig. 84. *Lithancylus* sp. SAM–PCM5436. Parts of the suture line. × 1,5.

Helicancyloceras (*Nonyaniceras*) spp. fragments

Several fragments are definitely referable to the genus, but are too fragmentary or poorly preserved to merit specific status. SAS Z8(7) (Fig. 81A, C) shows that coiling may have been very loose in some species.

SAS H71D/15 (Fig. 81B) seems to represent the aperture of a small helix.

Two very worn specimens, SAM–PCZ5504 (Figs 83C–D, 78D) and BMNH C79162 (Fig. 68G–H) have ribbing very similar to that of *H.* (*N.*) *circulare*, but have very strongly developed trituberculate ribs. The ventral tubercles are largest and the umbilical ones smallest and pointed.

Incertae sedis

Two specimens from the Upper Aptian of the Mfongozi Creek cannot be referred with certainty to any ancyloceratid genus. Z8(1) (Fig. 85A–B) is part of a phragmocone with definite impressions of tubercles on the dorsum. Ornament consists of slightly sinusoidal ribs separated by narrow interspaces. At the smaller end there is a distinct interruption of ribbing over the venter, but at the larger there is no trace of this. The suture line is partially exposed, showing a large, bifid E/L saddle, a long, narrow trifid L and a very small trifid U.

The impression of tubercles on the dorsum and the ribbing in general is reminiscent of specimens of *A.* (*Adouliceras*) *mozambiquense*, but the former is a Lower Aptian species. It could possibly be an australiceratid.

Z8n (Fig. 86) is a J-shaped fragment of an uncoiled ancyloceratid ammonite. Ornament is very weak, consisting of very weak ribs which are radial over the flanks and curve broadly forward over the dorsum. Ribbing is absent on part of the internal mould. The whorl section is more or less oval throughout. Again affinities with the Early Aptian uncoiled forms of *A.* (*Adouliceras*), *Tropaeum* and *Australiceras* have to be ruled out because of its occurrence in the Upper Aptian. Egojan (1974) recently described Upper Aptian uncoiled ammonites from the Caucasus, which he referred to a new family, Epacrioceratidae. The main characteristic of the family is the presence of a bipartite lateral lobe (L) and a smaller trifid U and I. In the present specimen the lateral lobe is distinctly asymmetric (Fig. 80B) but is more trifid than bifid. On the basis of the limited material further speculation on the affinity of the Zululand specimen with the Caucasian material serves little purpose.

PALAEOBIOGEOGRAPHY

The distribution of the Aptian ammonoid genera *Ancyloceras* (*Adouliceras*), *Tropaeum*, *Australiceras*, *Lithancylus*, *Toxoceratoides* and *Tonohamites* is summarized in Figure 89.

The sources of these data are as follows:

Lithancylus Casey 1961 (England & Tyrol); Anderson 1938 (California); Day 1974 (Australia); Leanza 1970 (Patagonia); Thomson 1974 (Alexander Island).

Fig. 85. Insertae sedis. SAS Z8(1) from locality 186, Zululand, Aptian III–IV. × 1,3.

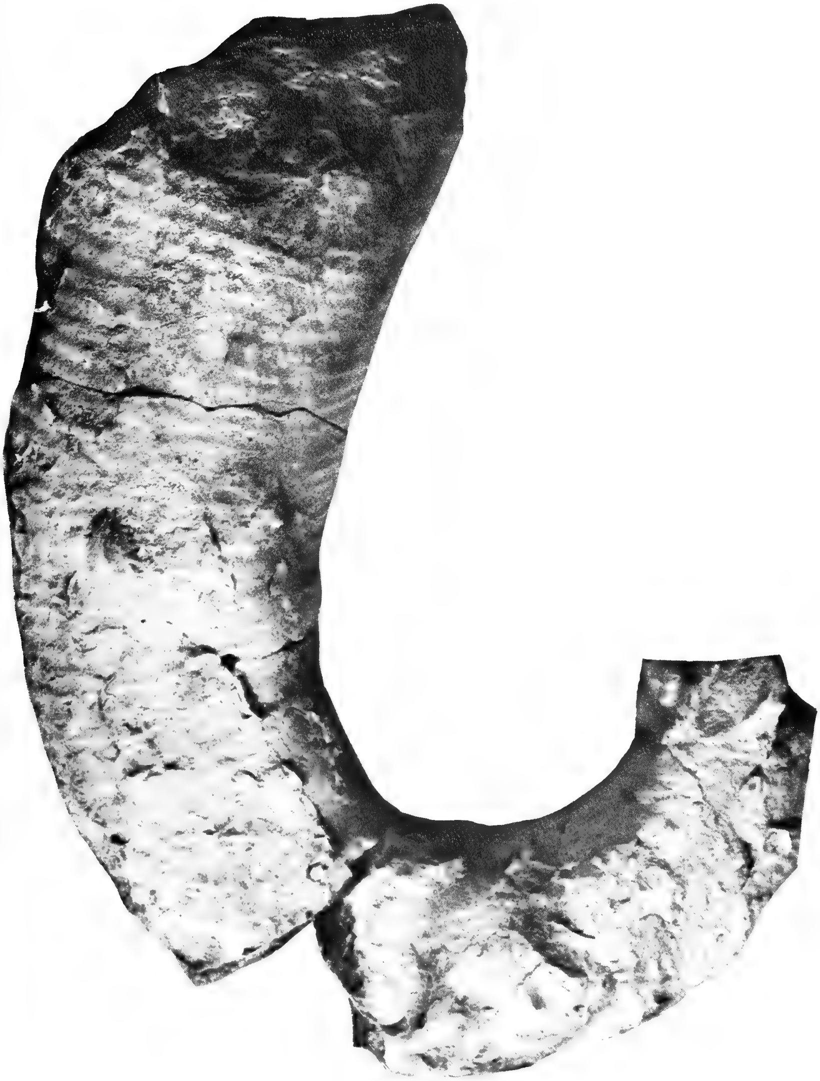


Fig. 86. Insertae sedis. SAS Z8n from locality 186, Aptian III–IV. × 0,5.

Tropaeum Casey 1960 (England); Sinzow 1872, 1905 (Caucasus); Von Koenen 1902 (Northern Germany); Dimitrova 1967 (Bulgaria); Stolley 1912, Frebold 1935 (Spitzbergen); Spath 1946 (Greenland); Jeletzky 1964 (Arctic Canada); Nakai 1968, Obata *et al* 1975 (Japan); Wilckens 1947 (south Georgia, Antarctica); Leanza 1963 (Patagonia?); Da Silva 1962 (Mozambique); Haughton 1936 (Zululand); Thomson 1974 (Alexander Island?); Etheridge 1909; Whitehouse 1926; Day 1974 (Australia); Royo y Gomez 1945 (Columbia); Spath 1931 (India); Förster 1975*a* (Mozambique).

Australiceras Casey 1960, 1961 (England); Sinzow 1905 (Caucasus); Dimitrova 1967 (Bulgaria?); Royo y Gomez 1945 (Columbia); Waagen 1875 (India); Anderson 1938 (California); Favre 1908 (Patagonia?); Thomson 1974 (Alexander Island); Haughton 1936; Kennedy & Klinger 1975 (Zululand); Förster 1975*a* (Mozambique); Obata *et al.* 1975 (Japan).

Tonohamites Casey 1961 (England); Von Koenen 1902 (northern Germany); Collignon 1962 (Madagascar); Kennedy & Klinger 1975 and herein (Zululand).

Toxoceratoides Casey 1961 (Western Europe); Förster 1975*a* (Mozambique); Thomson 1974 (Alexander Islands); Murphy 1975 (California).

Ancyloceras (*Adouliceras*) Thomel 1964 (France); Anderson 1938 (California and Oregon?); Dames 1880 (Germany); Zululand (herein).

Interpretation of data

The main picture that emerges, not only from the map, but from the systematic descriptions, is the close relationship between the faunas of the southern part of European U.S.S.R. and Western Europe, and Zululand and Mozambique. Open marine connections clearly existed in both Aptian and Barremian times between Tethys and the eastern parts of Africa and India, to facilitate free migration.

The most primitive forms of *Tropaeum*, *Australiceras* and *Ancyloceras*, are

Fig. 87. Suture line of *Tropaeum subsimbirsteense compressum*. × 1.

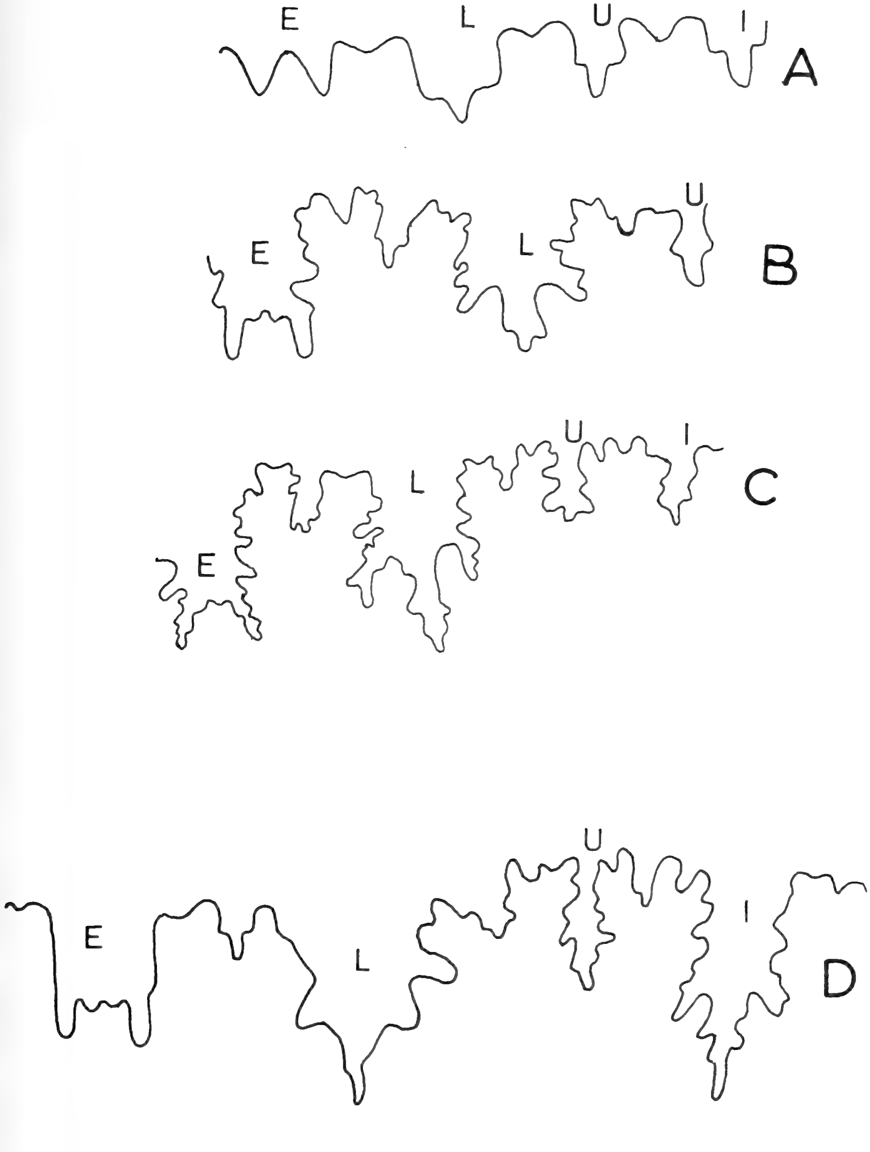
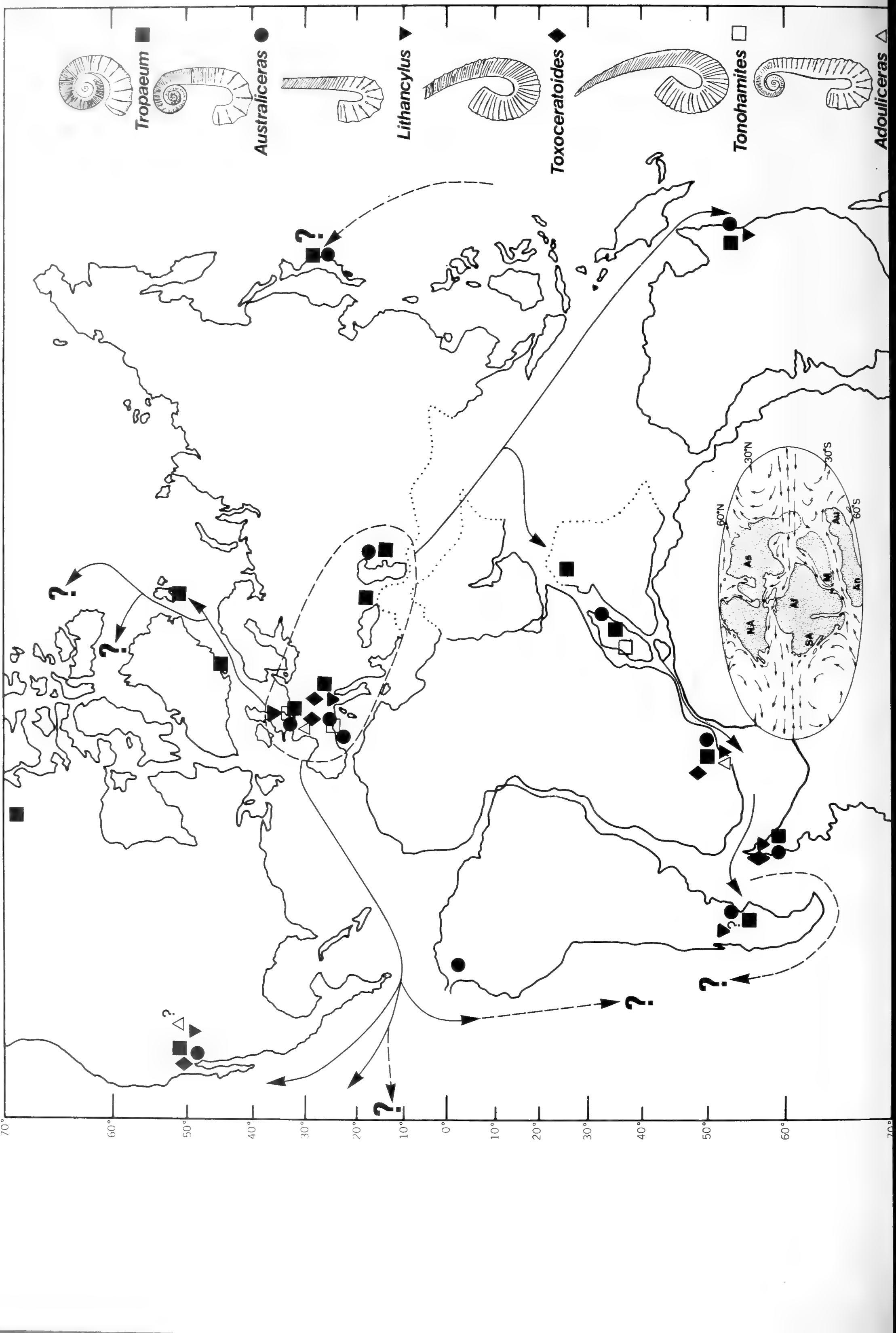


Fig. 88. A–C. Suture lines of *Helicancyloceras* (*Helicancyloceras*) *vohimaranitraensis* (Collignon, 1962) from unnumbered fragments. × 6. D. Suture line of *Tonohamites aequicingulatus* (von Koenen, 1902). SAS Z8/Ta1. × 6.


Tropaeum ■
Australiceras ●
Lithancylus ▼
Toxoceratoides ◆
Tonohamites □
Adouliceras △
?
70°
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to be found in the region ranging east–west from Great Britain to east of the Caspian Sea, and current evidence suggests this as the source area of the group, genera migrating from there to other parts of the world during early Cretaceous time. There is great similarity between the faunas of Zululand and Mozambique and those of Madagascar, India, Australia and to a lesser extent south-eastern South America and the Antarctic regions. There is little similarity, however, with the west coast faunas of the Americas.

Part of the dispersal pattern shown in Figure 89 may be explained by taking ocean currents prevailing during the Early Cretaceous into account. A study of this kind was recently undertaken by Gordon (1973), the results of which are here briefly summarized and illustrated in the insert in Figure 89. Due to the absence of the Panama Isthmus, a westward-flowing circumglobal tropical current existed. Apart from assisting in distributing heat around the globe, the equatorial current was forced northwards into the Tethyan region by the bulge of Africa–Arabia. By this mechanism the Tethyan fauna was distributed around the globe. Water from this current was probably deflected southwards along the eastern coast of Africa by the 'horn' of Africa, past Mozambique and Zululand. Due to the higher temperature of this current, the Tethyan faunas could survive at these high latitudes. The absence of comparable faunas on the west coast of South America seems to indicate the presence of a cold current flowing equatorialward. Due to west-wind drift, an eastward-flowing current must have existed at high latitudes in the Southern hemisphere. Due to the mixing of the Antarctic current and the southward-flowing water from the equator, a low temperature differential existed, allowing part of the Tethyan fauna to be distributed eastwards. This may explain the similarities between the faunas of the southern parts of South America, the Antarctic regions, south-east Africa, Madagascar, India and Australia. The similarity between the south-east African and Australasian fauna becomes even more obvious during the Albian as shown by the distribution of the labeceratids, or during the Maastrichtian by the eubaculitids.

It is also interesting to note that, apart from the Columbian occurrence of *Australiceras*, the majority of ancyloceratids appear to have lived in temperate regions between latitudes 20 to 60 degrees.

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Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

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Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family **Nuculanidae**

Nuculana (*Lembulus*) *bicuspidata* (Gould, 1845)

Figs 14–15A

Nucula (*Leda*) *bicuspidata* Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

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In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

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SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

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HERBERT CHRISTIAN KLINGER
&
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CRETACEOUS FAUNAS FROM ZULULAND, SOUTH AFRICA AND SOUTHERN MOZAMBIQUE THE APTIAN ANCYLOCERATIDAE (AMMONOIDEA)

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Kohn, A. J. 1960*a*. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) **2**: 309–320.
Kohn, A. J. 1960*b*. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* **17** (4): 1–51.
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(continued inside back cover)

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A NEW SPECIES OF *HALICYCLOPS* (COPEPODA, CYCLOPOIDA) FROM ESTUARIES IN TRANSKEI, SOUTHERN AFRICA

By

T. WOOLDRIDGE

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A NEW SPECIES OF *HALICYCLOPS* (COPEPODA, CYCLOPOIDA) FROM ESTUARIES IN TRANSKEI, SOUTHERN AFRICA

By

T. Wooldridge

Department of Zoology, University of Port Elizabeth

(With 3 figures and 1 table)

[*MS. accepted 28 April 1977*]

ABSTRACT

A new species of the genus *Halicyclops* Norman, 1903 is described and illustrated from estuaries in Transkei, southern Africa. The species, *Halicyclops pondoensis*, is closely allied to *H. neglectus*, *H. rotundipes* and *H. higoensis*. It is distinguished from these three forms particularly in regard to the fourth and fifth pair of legs. In *H. pondoensis* hair-like structures are present in the proximal part of the seta of the first endopodite segment of leg 4. These hair-like structures are absent in other species. Two spines and three setae are present on leg 5 of the male of *H. pondoensis*. In *H. neglectus*, *H. rotundipes* and *H. higoensis* the male 5th leg bears three spines and two setae. In the present species the second segment of the 5th leg in both the male and female is elongated.

A key to the species recorded from the African continent south of the Tropic of Cancer, and from the islands of Madagascar and Réunion, is given.

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INTRODUCTION

A new species of the cyclopoid copepod genus *Halicyclops* was found in plankton samples collected from estuaries on the east coast of southern Africa. The genus has a world-wide distribution and is recorded from marine, brackish and fresh-water habitats. Although most species are free-living, a number are reported from the interstitial fauna of marine beaches. Species of *Halicyclops* are also found on the body surface or in the tubes of polychaete worms. *Halicyclops caridophilus* inhabits the gill chamber of the mudlobster, *Thalassina anomala*.

The genus is so far known from 47 described forms. The present species is the first member of the genus described from estuaries in southern Africa, although Hill (1966) tentatively recorded *H. pilifer* from the Umlalazi estuary (28°57′S), Zululand. The new species of *Halicyclops* reported here is recorded

Ann S. Afr. Mus. 73(10), 1977: 361–371, 3 figs, 1 table.

from Msikaba estuary (31°19′S) and Mbotyi estuary (31°28′S) on the Pondoland coast, Transkei. Specimens were taken at all seasons from May 1972 to March 1973 in plankton tows collected from just below the water surface in salinities ranging from 1–33‰.

DESCRIPTION OF MATERIAL

Halicyclops pondoensis sp. nov.

Figs 1–3

HOLOTYPE

SAM–A15614 in the South African Museum, Cape Town. Adult female from Mbotyi estuary on the Pondoland coast (31°28′S), collected by T. Wooldridge, 29 November 1972.

PARATYPES

SAM–A15614 in the South African Museum, Cape Town. Numerous adult males and adult females from Mbotyi estuary on the Pondoland coast (31°28′S), collected by T. Wooldridge, 29 November 1972.

Description

Female. Total length 0,61–0,68 mm (mean of five specimens 0,65 mm). Metasome about twice the length of the urosome. Rostrum small, bluntly triangular, curved ventrally and posteriorly, and hence not visible from the dorsal side.

Cephalic segment bluntly rounded anteriorly, wider than long (1,25–1,33 : 1), the greatest width in the posterior region (Fig. 1A). Second thoracic segment longer than third and fourth respectively, which are equal in length. The posterior lateral edges of second and third segments free, angular; those of the fourth segment free but more rounded. Fifth thoracic segment short, its posterior lateral margins bluntly pointed and bearing the fifth pair of legs.

Genital segment (Fig. 2A) with small protrusions on the anterior lateral margin. Length subequal to the width. Urosomal segments posterior to genital segment progressively shorter and narrower, the anal segment with a deep medial incision. Posterior border of the first three segments of urosome denticulate. Anal segment serrated on the posterior ventral border only. A row of fine spinules on anterior dorsal side of the anal segment.

Furcal rami (Fig. 2A) slightly longer than wide and about equal in length to the anal segment. All furcal setae usually found in the genus present, the proximal dorso-lateral seta reaching slightly beyond furca. Dorsal seta about twice the length of the dorso-lateral seta, arising from the inner posterior region. Ornamented basally with minute spinules. Apical setae long and stout, the inner as long or slightly longer than the length of the metasome, the outer less than half as long. Proximal half of shorter and less stout seta spinose on its outer margin only, distal half plumose, ornamented basally on dorsal surface by a row

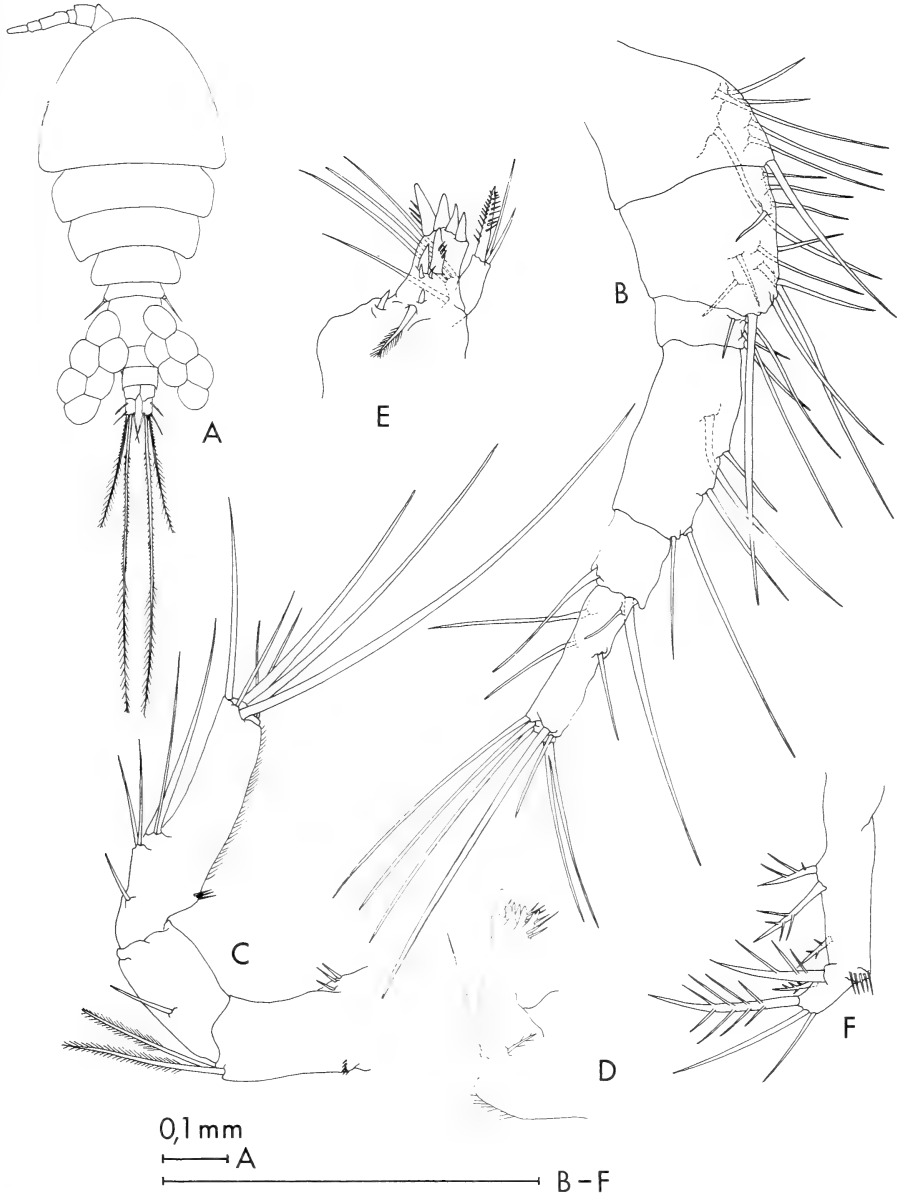

Fig. 1. Female. A. 0,62 mm female. B. Antennule. C. Antenna. D. Mandible. E. Maxilla 1. F. Maxilliped.

of short spinules. Inner apical seta spinose on lateral margins in proximal half, the spines becoming less sparse posteriorly. Terminal half plumose. Innermost furcal seta short, about one-third the length of ramus. Outermost seta non-plumose, about one and a half times length of ramus.

Antennule six segmented (Fig. 1B), almost half as long as cephalic segment. Ultimate and penultimate segment combined slightly longer than anti-penultimate segment. Setation and relative lengths illustrated in Figure 1B. Aesthetask present on distal margin of ultimate segment.

Antenna three segmented (Fig. 1C), with two setae on anterior lateral border of first segment. Inner lateral margin with a number of short spines. Second segment with one seta. Third segment about three and a half times as long as broad, bearing five lateral setae. Two lateral setae, of which one is relatively stout, born on raised portion midway along length of segment. Terminal group consisting of three slender and four stout setae, the longest placed sub-terminally. A row of fine spinules along inner lateral border of ultimate segment.

Mandible slender (Fig. 1D), with seven irregular teeth terminally. Outer basal area with a long and a shorter plumose seta.

Maxilla 1 bilobed (Fig. 1E), with broad basal segment. Inner lobe with four apical teeth, the posterior lateral tooth longer and more robust. Dorsal surface bearing four short and two large robust teeth. A plumose seta on inner, proximal border. Outer lobe or palp with four lateral, non-plumose setae, the three distal teeth borne on a slightly produced lobe. Apex of palp bearing a barber spine and two slender setae.

Maxilla 2 (Fig. 2B), largest of oral appendages. First and second segment bearing two plumose, and a single non-plumose seta respectively. Third segment modified, expanded and produced into two stout serrated claws and a single non-plumose seta Attenuated lacinia between second and third segments, bearing a smooth spine in mid-region, and three more on distal half. Terminal segment slightly wider than long, with two stout, serrated claws, two hair-like setae and a smooth spine.

Maxilliped slender (Fig. 1F), basal segment with three attenuated spines along inner lateral margin. Terminal segment less than half as long as basal, with two attenuated spines on inner lateral margin. More proximal spine robust and long. Distal margin bears a claw-like attenuated spine and two subterminal setae the longer equal in length to the terminal spine and about two and a half times as long as apical segment.

Swimming legs 1–4 biramous (Figs 2C–D, 3A), first basipodite segment bearing seta on inner margin, the second with seta on outer margin. Distal margin of second basipodite segment of first four pairs of legs with fine spinules. Exopodite and endopodite three segmented, the second podomere shorter than the first and third, more pronounced on exopodite. Outer lateral margins of endopodite segments of legs 1–4 with fine, hair-like setae.

First pair of legs (Fig. 2C) smaller than succeeding pairs, the second basi-

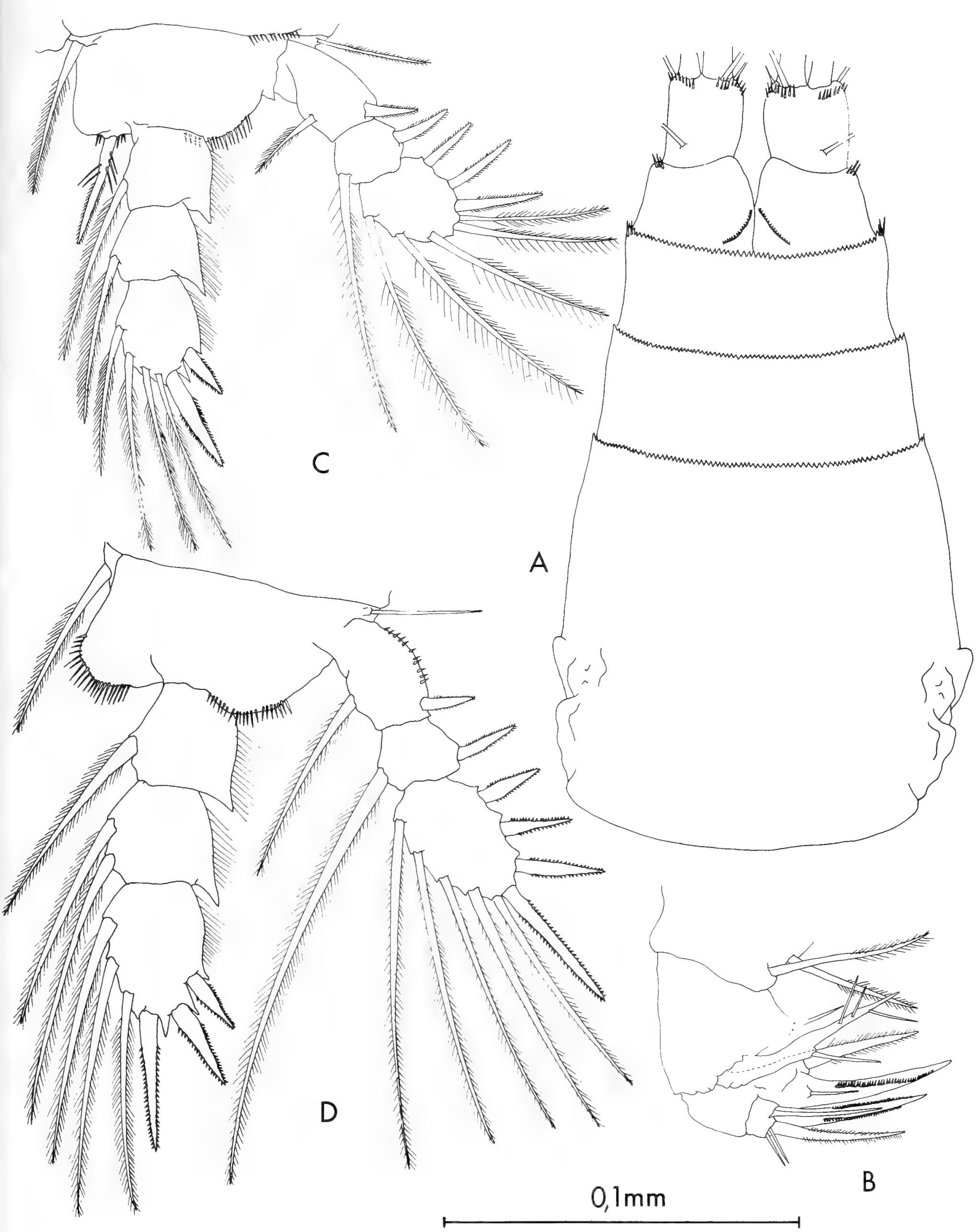

Fig. 2. Female. A. Abdomen. B. Maxilla 2. C. Leg 1. D. Leg 2.

podite segment with a stout, serrated spine on inner distal margin, reaching to about the mid-point of the endopodite. Proximal region of spine bearing a number of smooth setae, the number and relative lengths showing individual variation. First exopodite segment with one serrated spine and one short plumose seta. Second exopodite segment with one serrated spine and one long plumose setae. First and second endopodite segments each with a single plumose seta. Third segment with sharp, spine-like distal corners and bearing two serrate spines and four plumose setae.

Second and third pairs of legs similar, the ornamentation as follows: first and second exopodite segment each with a serrated spine and one plumose seta (Fig. 2D). Apical segment with three lateral spines, one long terminal spine and five plumose setae. Outer lateral border of first exopodite of second leg with fine spinules. These spinules present on first and second exopodite segment of third pair of legs. First endopodite segment with one plumose seta, second segment with two plumose setae and apical segment with three plumose setae, two terminal spines and one lateral spine. Exopodite and endopodite spines all serrated. Terminal segment with sharp distal corners.

Fourth pair of legs similar to preceding two pairs, but showing differences in ornamentation of the terminal segments and in the structure of the seta of first endopodite segment (Fig. 3A). Exopodite three with five plumose setae, two lateral spines and one terminal spine. Outer lateral border with minute spinules. Terminal segment of endopodite with one lateral spine, two terminal spines and two inner plumose setae. Seta of first endopodite segment with about eight long, slender hairs in proximal region.

Leg 5 (Fig. 3B) with first segment fused with thoracic segment, bearing a long, smooth seta on a basal protuberance. Protuberance ornamented with a row of fine spinules. Second segment about one and three-quarters as long as wide. Inner lateral margin straight, with one subterminal, finely serrated spine. Length of this spine distinctly less than length of second segment. Terminal seta long and slender, about twice the length of inner spine. Outer margin with two finely serrated spines, the more proximal always the longest and about equal in length to the second segment. All spines relatively slender. Origin of terminal seta almost equidistant between two subterminal spines. Second segment with a number of rows of fine spinules, their relative positions illustrated in Figure 3B.

Male. General body form similar to female, but smaller in size (Fig. 3C). Total length 0,49–0,53 mm (mean of eight specimens 0,51 mm). Urosome slender, five segmented. Anal segment and caudal furcae as in female.

Antennule of about thirteen segments (Fig. 3D), prehensile. Segments difficult to define. Structure and arrangement of setae illustrated in Figure 3D. Remaining cephalic appendages and legs 1–4 as in female.

Leg 5 first segment and ornamentation similar to female (Fig. 3E). Second segment about twice as long as wide, inner margin straight, with two slender plumose setae in distal half. Setae slightly longer than second segment. Terminal setae distinctly plumose and almost twice as long as second segment. Rounded

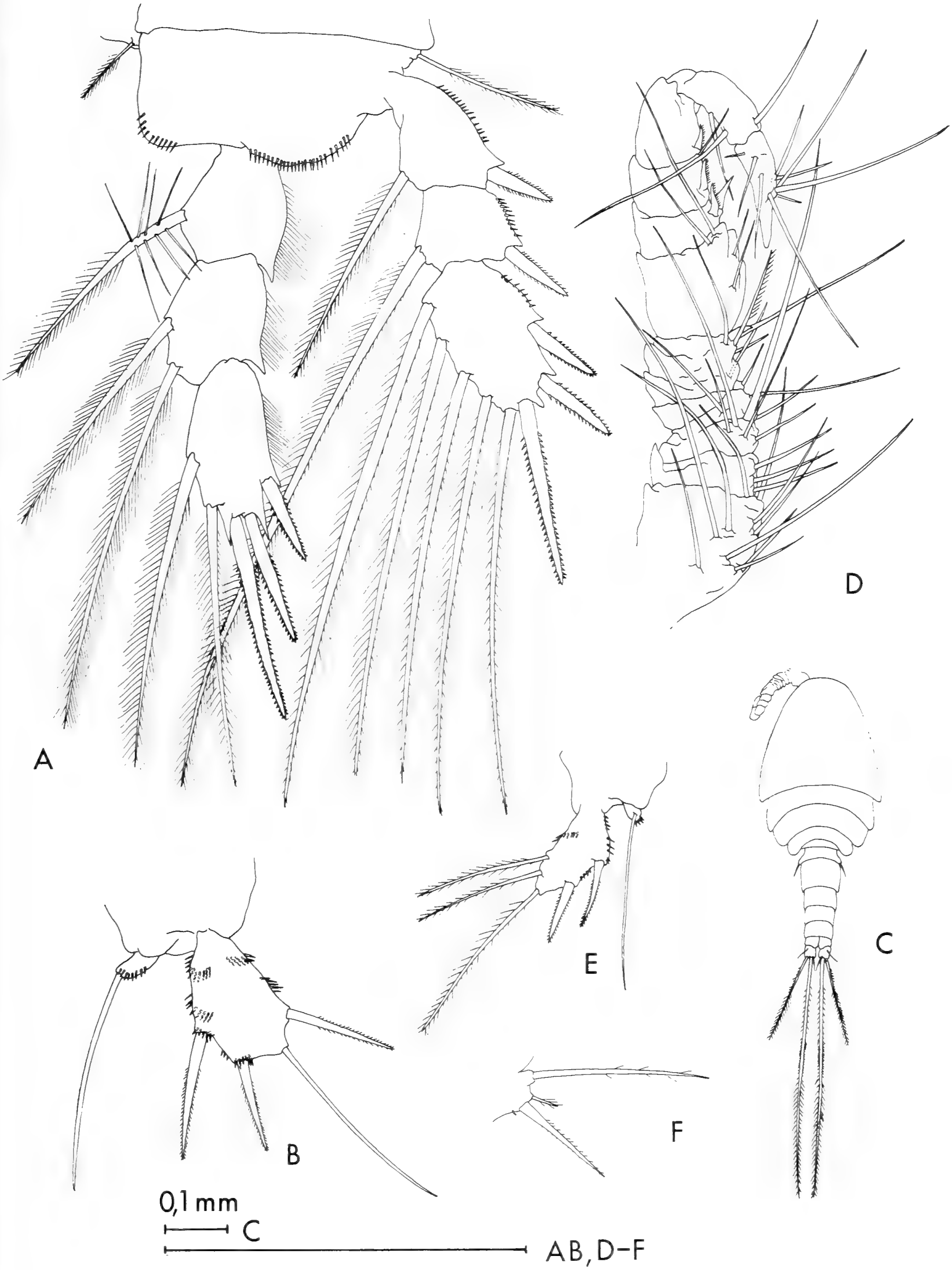

Fig. 3. A–B. Female. A. Leg 4. B. Leg 5. C–F. Male. C. 0,49 mm male. D. Antennule. E. Leg 5. F. Leg 6.

outer lateral margin with two short, finely serrated, slender spines. Length of spines about half the length of lateral setae on the inner border of segment. Margin of segment with a number of fine spinules.

Leg 6 (Fig. 3F) with a plumose outer seta almost equal in length to terminal seta of leg 5, borne on a produced lobe. Inner lobe broad, bearing a sharp serrated spine and a short spine-like seta.

DISCUSSION

The genus *Halicyclops* Norman, 1903 is widely scattered geographically and is known from forty-seven described species. A key to the species by Lindberg (1957) and a paper by Wilson (1958) were valuable aids to workers and did much to emphasize important diagnostic characteristics. At the time of Lindberg's (1957) publication, thirty-three species of the genus had been described. A further ten species were noted by Kiefer (1967). To this list must be added *Halicyclops ryukyuensis* Ito, 1962, *H. latus* Chia-Jui & Ai-Yun, 1964, *H. ambiguus* Kiefer, 1967, and *Halicyclops longispinosus* Monchenko, 1974.

The present species differs from those already described, but shows similarities to *H. neglectus* Kiefer, 1935 (redescription: Kiefer 1936; Candeias 1964); to *H. rotundipes* Kiefer, 1935 (redescription: Kiefer 1936; Plesa 1956; Petkovski 1955 as *H. neglectus rotundipes*); and to *H. higoensis* Ito, 1958. *H. neglectus* and *H. rotundipes* are no doubt closely allied and Wilson (1958) suggests that the two forms may be synonymous.

Halicyclops pondoensis differs from *H. neglectus*, *H. rotundipes* and *H. higoensis* particularly in regard to the fourth and fifth pair of legs. In *H. pondoensis* the seta on the first endopodite segment of the fourth pair of legs in the male and female bears hair-like structures in the proximal region. These hair-like structures are absent in other species.

The inner proximal seta on the third endopodite segment of the fourth pair of legs differs in *H. higoensis*. In *H. pondoensis*, *H. neglectus* and *H. rotundipes* a typical seta is present. *H. higoensis* is distinguished in having this seta in the form of a spine.

Important differences between the species are also found on the fifth pair of legs. In *H. neglectus* and *H. rotundipes* the second segment in both the male and female is rounded. In *H. higoensis* this segment is slightly elongated. In *H. pondoensis* the second segment in the female is about one and three-quarters as long as wide and about twice as long as wide in the male. The armature on this segment in the male is also characteristic. In *H. pondoensis* there are two spines and three setae. In *H. neglectus*, *H. rotundipes* and *H. higoensis* three spines and two setae are present.

The armature of the sixth pair of legs in the male also shows important differences between the species. In *H. neglectus*, *H. rotundipes* and *H. pondoensis* the spine on leg six is relatively long and slender. In *H. higoensis* this spine is stout. Two setae are also present on leg six and in *H. higoensis*, *H. neglectus* and

H. rotundipes the outermost seta is slightly longer than the inner seta. In *H. pondoensis* the inner seta is short and spine-like.

Small differences between the species are also apparent in the form of the genital segment. In *H. neglectus* and *H. rotundipes* the lateral protrusions are well marked, while in *H. pondoensis* and *H. higoensis* these protrusions are small.

The main differences separating these four species are summarized in Table 1.

H. pondoensis is the fourth member of the genus to be described from the continent of Africa south of the Tropic of Cancer. A further four species are known from the islands of Madagascar and Réunion. A key to these eight species with their geographical distribution is given.

TABLE 1

Summary of important differences separating *H. pondoensis* from three closely allied forms.

	Halicyclops neglectus	*Halicyclops rotundipes*	*Halicyclops higoensis*	*Halicyclops pondoensis*
Seta on first endopodite segment of leg four, male and female	Typical seta present	Typical seta present	Typical seta present	Seta with hair-like structures in proximal region
Inner proximal seta on third endopodite segment of leg four, male and female	Typical seta present	Typical seta present	Spine present	Typical seta present
Second segment of fifth pair of legs in male and female	Rounded	Rounded	Slightly longer than round	One and three-quarters as long as wide in female and twice as long as wide in male
Armature of leg five in male	Three spines and two setae present	Three spines and two setae present	Three spines and two setae present	Two spines and three setae present
Armature of leg six in male	Spine long and slender	Spine long and slender	Spine short and stout	Spine long and slender
	Outermost seta slightly longer than inner seta	Outermost seta slightly longer than inner seta	Outermost seta slightly longer than inner seta	Outermost seta much longer than inner seta which is spine-like
Genital segment	Lateral protrusions well marked	Lateral protrusions well marked	Lateral protrusions small	Lateral protrusions small
Total body length:				
Male	390–440 μm	460 μm	460 μm	490–530 μm
Female	600 μm	500–560 μm	520 μm	610–680 μm

KEY TO THE SPECIES OF *HALICYCLOPS* FROM THE CONTINENT OF AFRICA SOUTH OF THE TROPIC OF CANCER AND FROM THE ISLANDS OF MADAGASCAR AND RÉUNION WITH A NOTE ON THEIR DISTRIBUTION

1. Inner seta absent on endopod segment 3 of leg 4 *H. korodiensis* Onabamiro, 1952
Distribution: Nigeria.

– Inner seta present on endopod segment 3 of leg 4 2

2. Spines along posterior dorsal edge of penultimate abdominal segment longer in the middle region than on the sides 3

– Spines along posterior dorsal edge of penultimate abdominal segment equal in length 6

3. Spine formula on terminal exopod segments of legs 1–4, 2.3.3.3. Furcal rami about as long as broad .. .. *H. pusillus* Kiefer, 1954
Interstitial, Manoantsetra lagoon, Madagascar.

– Spine formula on terminal exopod segments of legs 1–4, 3.4.4.3. Furcal rami longer than broad 4

4. Chitinous spine present on each side of genital segment.. *H. thermophilus* Kiefer, 1929
In a limestone cave, Madagascar (Lindberg 1952).

– No chitinous spine present on each side of genital segment 5

5. Furcal rami at least 2 times as long as broad. Spines along the posterior dorsal edge of penultimate abdominal segment extremely long in the middle region, reaching beyond midlength of anal segment .. .. *H. denticulatus* Kiefer, 1960
Brackish water near Manambato, Madagascar.

– Furcal rami about 1,5 times as long as broad. Spines along the posterior dorsal edge of penultimate abdominal segment slightly longer in the middle region than on the sides, not reaching beyond midlength of anal segment .. *H. reunionis* Kiefer, 1960
Island of Réunion.

6. Genital segment broader than long .. .. *H. gauldii* Plesa, 1961
Interstitial: Lighthouse Beach, Accra, Ghana.

– Genital segment about as long as broad 7

7. Genital segment with small lateral protrusions. Furcal rami about as long as broad. Hair-like structures on distal part of seta of 1st endopodite segment of leg 4. Three spines and a single seta on second segment on leg 5 of female. Two spines and three setae present on leg 5 in male .. .. *H. pondoensis* sp. nov.
Pondoland estuaries, Transkei. Planktonic.

– Genital segment without lateral protrusions, or at most, a weak projection present. Furcal rami about 1,5 times as long as broad. No hair-like structures on seta of 1st endopodite segment of leg 4. Three spines and a single seta on second segment of leg 5 of female. Male undescribed .. .. .. *H. orae eburnensis* Lindberg, 1957
Ebrie lagoon, Ivory Coast.

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6. SYSTEMATIC papers must conform with the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (figs 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:
comma separates author's name and year
semicolon separates more than one reference by the same author
full stop separates references by different authors
figures of plates are enclosed in parentheses to distinguish them from text-figures
dash, not comma, separates consecutive numbers

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33°51′S 25°39′E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

7. SPECIAL HOUSE RULES

Capital initial letters

(a) The Figures, Maps and Tables of the paper when referred to in the text
e.g. '. . . the Figure depicting *C. namacolus* . . .'; '. . . in *C. namacolus* (Fig. 10) . . .'

(b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names
e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene

(c) Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as
'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

T. WOOLDRIDGE

A NEW SPECIES OF *HALICYCLOPS* (COPEPODA, CYCLOPOIDA) FROM ESTUARIES IN TRANSKEI, SOUTHERN AFRICA